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CORNEAL INJURIES IN THE ATLANTIC STINGRAY *DASYATIS SABINA* (LESUEUR)[1]

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ABSTRACT

Stingrays *Dasyatis sabina* (Lesueur), captured inshore near Port Aransas, Texas from February to April, had cloudy corneas. This condition was produced by irregularities in the epithelial covering. These contained patches of sloughed and degenerate cells, cellular debris, pits and holes containing degenerating cells and strands of regenerating cells. Most injuries were on the external surface; some were on the inner surface. The degree of injury and cloudiness varied greatly over the cornea. Targets viewed through cloudy regions of corneas appeared fuzzy, and visual acuity (to the human observer) was 0.25 to 1. Maximal resolving power of the stingray's eye, estimated from spacing of cones, is 6′, and it is likely that the limit of photopic visual acuity is determined more by retinal grain than by defective cornea. Inshore waters are often very turbid and carry a heavy silt load. Corneal injury is probably caused by suspended particles, and high turbidity greatly reduces sighting distances.

INTRODUCTION

While dissecting stingray eyes it was repeatedly observed that the cornea appeared cloudy. The stroma itself was clear, as could be readily observed by removing the epithelium; the cloudiness lay in the epithelial layer (Nicol 1978). Because such a common condition could profoundly affect visual acuity, a study was initiated of the stingray cornea.

MATERIALS AND METHODS

Stingrays *Dasyatis sabina* (Lesueur) were obtained in the Gulf of Mexico near Port Aransas. Some were trawled close to shore during February and April; others were captured during March by anglers fishing from the stone jetty. Fish were enucleated soon after capture; or were held in ponds provided with circulating sea water for periods up to two months, when their eyes were examined.

Microscopy

Fresh corneas in selachian Ringer (Nicholls 1933) were examined microscopically by transmitted light and superior illumination (Leitz Ultropak). For histological study eyes were preserved in Bouin's, Helly's and Zenker's fluids, and corneas were sectioned in paraffin wax at 8 μm. Peterfi's double embedding was used with some specimens. Sections were stained with

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Ehrlich's haemotoxylin, eosin and Biehbrich scarlet. Heidenhain's iron haemotoxylin and orange G, Mallory's triple, toluidine blue and thionine. Vital staining was done with 0.1% chlorazol black and 0.1% toluidine blue in selachian Ringer. Scanning electron micrographs were made of the surfaces of cornea fixed with 5% glutaraldhyde in 0.05M Na cacodylate buffer p.H. 7.2 + 25 mg % $CaCl_2$.

Measuring visual acuity

To obtain some measure of the clarity of the stingray's cornea, isolated corneas were immersed in selachian Ringer, and targets were viewed through them in selachian Ringer. The targets were Landolt's C's and black vertical stripes which were set at varying distances. They were regarded macroscopically and microscopically with a 3.2× objective and a 5× ocular. Target brightness was 520 mL.

OBSERVATIONS

Corneas of stingrays, both from fish freshly captured and those held in tanks, showed varying degrees of cloudiness (Fig. 1). To visual inspection the degree of cloudiness was not uniform, varying greatly over the cornea. When the epithelium was removed the stroma appeared clear and transparent.

Under microscopic examination, the epithelium showed cloudy patches here and there, where the outlines of hexagonal cells could be seen. Occasional individual cells and patches and streaks of cells stood out more prominently; exfoliating or desquamating cells were present (Figs. 2, 3, 8 to 11).

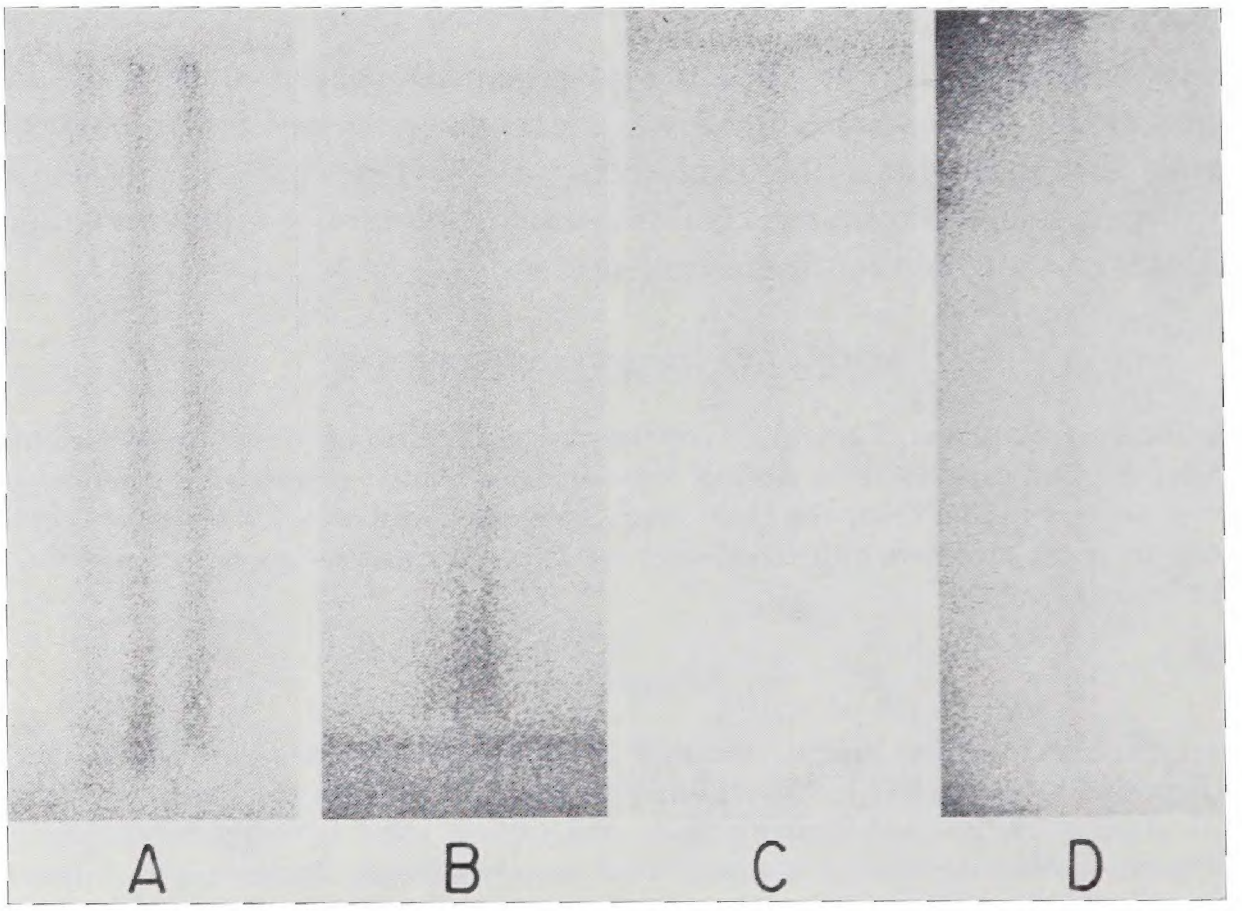
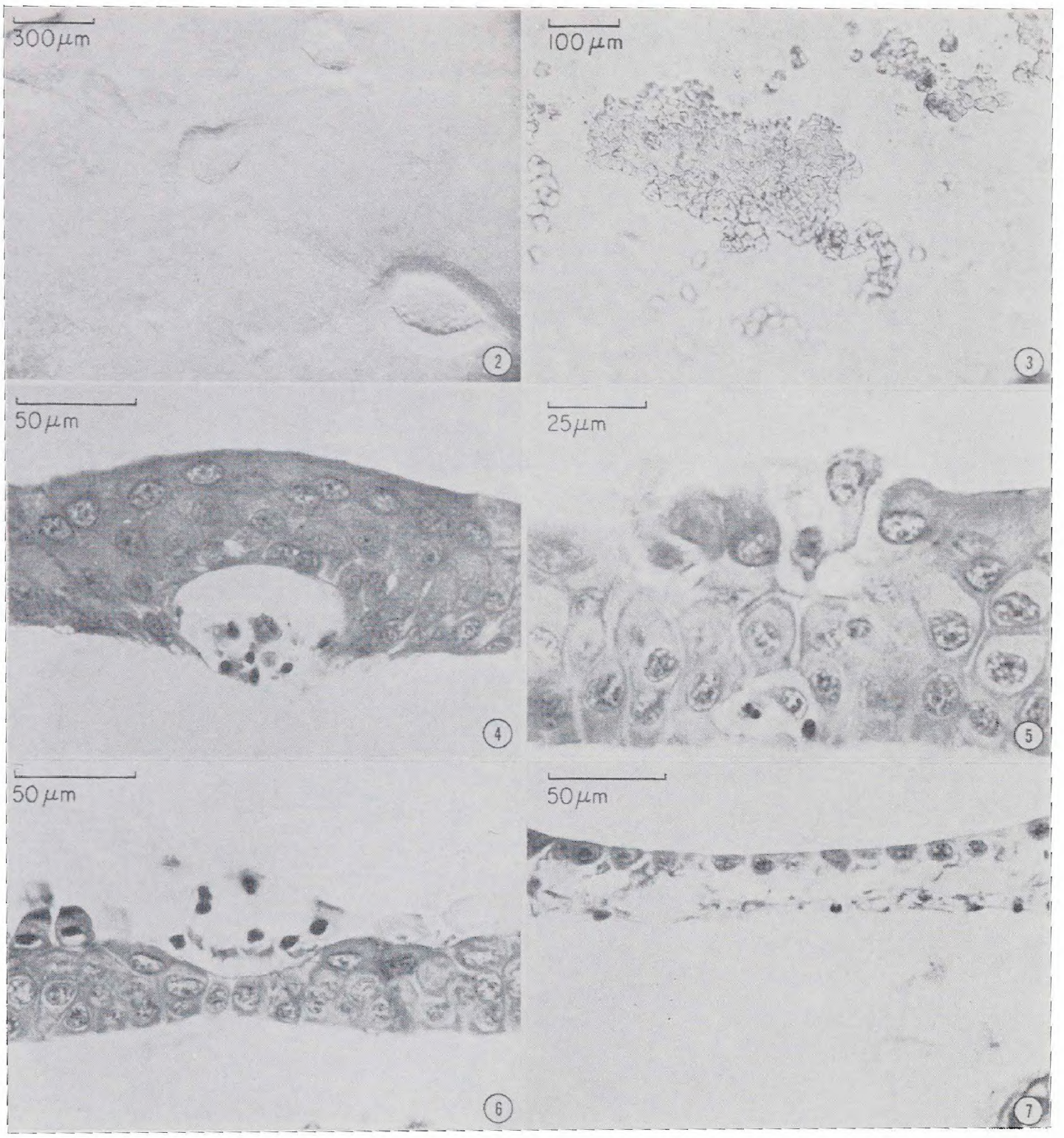


FIG. 1. Targets photographed through the cornea of a stingray. The targets were 1 m distant (from the cornea) and were three vertical lines, spacing and thickness equal. A, 5mm; B, 2.8mm; C, 1mm; D, 0.5mm spacing and thickness of lines.

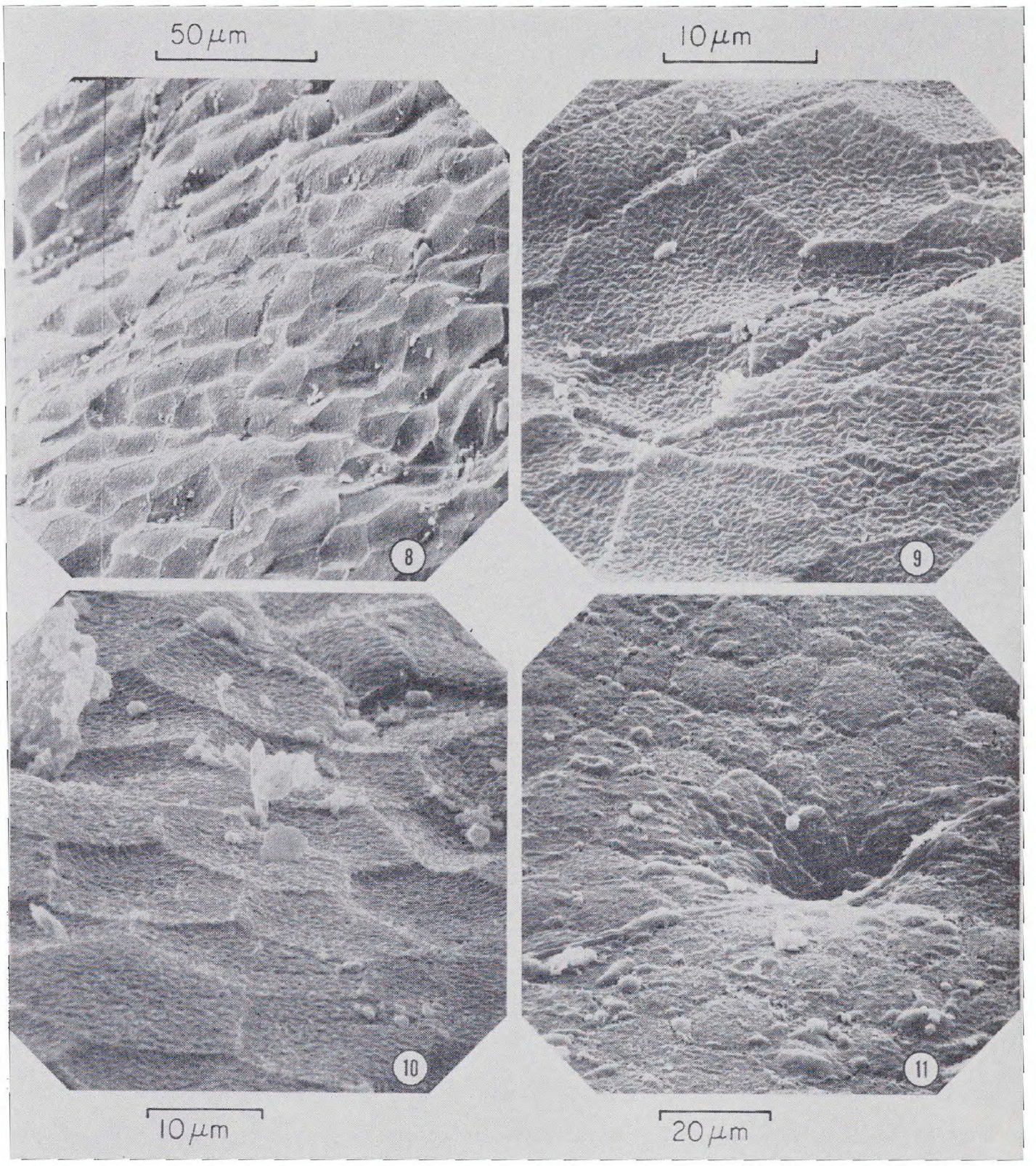


FIGS. 2 to 7. Surface views of corneas (2, 3), and transverse sections (4 to 7). Fig. 2, pits on the surface. Fig. 3, exfoliating cells. Fig. 4, cyst containing small cells inside the surface epithelium. Fig. 5, degenerate cells on the outside of the cornea. Note irregular cells on the inside. Fig. 6, cavity on surface containing sloughed cells. Fig. 7, a gap near the margin spanned by a single layer of cells.

HISTOLOGY

Preservation of the retina was best after Helly's, worst after Bouin's following which the cells appeared shrunken. Cells were somewhat shrunken after Zenker's; the staining was good. Staining was poor after Helly's and Bouin's. The epithelium was detached from the stroma after Bouin fixation and remained attached, at least in part, after Helly and Zenker fixation.

The following description is based upon examination of regions where the



FIGS. 8 to 11. Scanning electron micrographs of the corneal surface. The photographs show the shapes of the epithelial cells, microrugae, a pit (Fig. 11) and desquamated material (especially Fig. 10).

cornea appeared to be normal, that is to say when the epithelium and stroma were not obviously injured.

In the central cornea the epithelium contains four layers of cells. The basal layer of cells lies on Descemet's membrane, the cells are truncated cones, the apices of which alternate with cells of the next layer. The two middle layers contain roughly hexagonal cells, the outer layer is made up of cuboidal cells having conical inner faces alternating with cells of the third layer. Nuclei are large and contain three nucleoli. The cytoplasm is thin and granular. Each cell

possesses a more densely staining surround which is continued as a dense layer on the outer surface of the epithelium.

In the center of the cornea the epithelium is about equal to the stroma in thickness, approximately 50 μm. It is thicker towards the edges, about 960 μm.

The stroma consists of about thirty alternating layers or lamellae. The outer layer of the lamella is intricately joined to the basement membrane of the epithelium. Internally there are many fibroblasts. The inner surface is covered by endothelium. Vertical sutures, which join the lamellae together, are present. These are a common feature of the selachian cornea (Goldman and Benedek 1967).

The epithelia of freshly caught corneas bore many degenerate cells on both surfaces, but especially on the external surface (Figs. 4 to 6). Often the outer surface was undulatory, pitted, occasionally perforated, and sloughed cells were present. The corneas varied greatly in these respects. In some the outer surface was largely intact, generally smooth or somewhat undulatory. In others there were many irregularities amongst which were noted the following features: undulatory outer surface; concavities often containing sloughed cells with densely staining nuclei; pits containing a degenerate cell, sometimes protruding; irregular patches in which there were degenerate cells; sloughed cells and cellular debris; isolated degenerate cells or strings of the same on the surface. There were gaps, especially near the corneal margin, which contained cellular debris or which were covered in whole or in part by a thin layer of regenerating cells (one or two cells in thickness (Fig. 7)).

In electron micrographs, surfaces of the outer cells were covered with microrugae, and longitudinal striae coursed over the surface through series of cells (Figs. 8 to 10). These features have been observed in corneas of dogfish (Harding *et al.* 1974). Exfoliating cells, debris and pits are seen (Figs. 10 and 11).

Transparency

The minimal angle of resolution of targets by the observer when viewed through corneas of stingrays ranged from 1′ to 4′. There was no apparent improvement in clarity of the corneas the longer the fish were held captive in tanks. After two months in captivity, the minimal angle still ranged from 1′ to 4′ in air (40″ to 3′ 30″ in water). Resolution of the observer was slightly less than 1′, and resolution through the corneal stroma (cornea without epithelium) was 1′. Targets were fuzzy when viewed through cloudy corneas (Fig. 1), and it was not apparent that more information was being obtained by attempting to quantify transparency than could be secured by more subjective criteria.

Criteria for cloudy corneas used by Aurell and Holmgren (1953) were:

0, opaque
1, cloudy ink lines can hardly be seen
2, ink lines are cloudy, rather difficult to see
3, cloudy, ink lines fairly clear
4, somewhat cloudy, lines can be clearly seen
5, perfectly clear and transparent.

Corneas of three fish, caught by angling, were rated by these criteria:

Eye 1. 1 to 4 over the surface, least transparent in the center
Eye 2. 1 to 5, opaque in the center
Eye 3. 0 to 4, mostly 4
Eye 4. 0 to 4, mostly 4
Eye 5. 2 to 4
Eye 6. 0 to 4, opaque in the center

These observations show the great variation in transparency existing regionally over the corneal surface. The corneas of these fish were cloudy, and in no wise different from those of trawled animals.

DISCUSSION

The stingray's cornea has the usual histological features of the vertebrate cornea. The external surface is covered with epithelium continuous with the conjunctiva, and the stroma is continuous with the sclera. There is no secondary spectacle as in many teleosts. The stroma, as is usual among selachians, contains vertical sutures (Walls 1942, Rochon-Duvigneaud 1943, Gruber and Cohen 1978). Smelser (1961) has commented on the unusually clear demarcation of Bowman's membrane in the dogfish. Corneas of smooth hounds *Mustelus canis* and skates *Raja erinacea* are transparent. An unusual feature of the selachian cornea is that it is not hydrophilic, i.e. does not swell in water and retains its transparency (Smelser 1961, Goldman and Benedek 1967).

Some degree of corneal injury could have been caused by the violence of trawling. However, the eyes of fishes that were caught by angling were just as cloudy and had the same degree of injuries as had trawled fish. It is concluded that corneas of stingrays captured by either means were typical of fishes in their winter habitat.

Cloudiness in the corneas of Atlantic stringrays from the Gulf near Port Aransas is related to trauma of the external epithelium. It is produced either by surface irregularities, or intracellular changes, the nature of which await further study. These are large patches of desquamated cells, pits, incisures, denuded patches, cavities on the anterior, less often on the posterior surface of the stroma, and occasional flaws in the endothelium. The injuries are attributable to the benthic mode of life and heavy silt load of inshore waters, especially near the bottom. The animal, when swimming along the bottom, stirs up a cloud of sand and mud, which settles upon it when it comes to rest (Schultz 1944). In tanks the rays are constantly disturbing and swimming over one another. The bottoms of the tanks gather detritus, which is disturbed as the animals swim about. Under aquarian conditions the corneas of the stingrays are also exposed to abrasion by silt particles.

The cloudy cornea of the stingray introduces forward scattering into light path, and blurs the image. Underwater there is already a loss of energy from the line of sight between the object and the eye, and forward scattering of energy into the light path, causing reduction of contrast between the object and

the background. The inherent contrast of an object is reduced to an apparent contrast.

$$C_r = \frac{{}_tL_4 - {}_bL}{{}_bL}$$

where ${}_tL$ and ${}_bL$ are the brightness of object and background, and r is distance. Sighting ranges are short in turbid coastal waters. A range of 5m for dark objects is considered good in British inshore waters. Scuba divers (personal communication, J. Holland *et al.*) report that the visibility range nearshore in Gulf waters is often no more than 30 cm. A study has been made of transmissivity at an inshore station near Port Aransas. From November to May the depth at which light was reduced to 10% of surface intensity ranged from 2 to 11.5 m ($r = 0.20$ to 1.15) (Jones *et al.* 1965). In the turbid layer immediately over the bottom, the visibility range must be very short (Gazey 1970, Luria and Kinney 1970, Lythgoe 1971). Visibility distances are much greater in the shallow waters of the bays during calm days (sea state 0). These waters are frequented by stingrays in summer.

Cloudy corneas, by introducing an added degree of scattering into the light path from object to retina, further lower the contrast of the object, and make it more difficult to distinguish. It would be advantageous to place this on a realistic basis by pertinent measurements but, in lieu of the requisite environmental and behavoiral data, an estimate can be made of the maximal visual acuity of the stingray's eye under optimal photopic conditions. The resolving power (RP) of the retina depends upon two points in the visual field falling upon two separate cones, and can be calculated from the formula of Tamura and Wisby (1963), viz.

$$\sin \alpha = \frac{1}{F}\left(\frac{0.1\ (1 + 0.25)2}{\sqrt{n}}\right) \text{ min of arc,}$$

where F is Mathiessen's ratio (presumably applicable to the geometric axis) and n is the number of cones per 0.01 mm^2. For n = 69 (Hamasaki and Gruber 1965), α is 6′ and the visual acuity, 1/RP, = 0.167. This may be compared with the visual acuity of the average human observer of >1.

Visual acuity falls at low levels of luminance, in the human it is 0.7 at 1 ft L (ca 1 mL). We may expect acuity in the stingray to be further reduced at the very low levels of radiance obtaining in turbid waters (Foxell and Stevens 1955).

Although visual acuity is adversely affected by a cloudy cornea, the resolving power of the eye may be limited by retinal grain (i.e. cone density); and the ability to see an object, by its relative contrast under turbid environmental conditions.

ACKNOWLEDGMENTS

Dr. E. L. Thurston and staff of the Electron Microscope Center, Texas A&M University, are thanked for the scanning electron microscopy.

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GUANINE IN THE TAPETUM LUCIDUM OF THE LADYFISH, *ELOPS SAURUS* LINNAEUS[1]

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ABSTRACT

The eye of the ladyfish *Elops saurus* contains a retinal reflector (tapetum lucidum) composed of guanine crystals. There are 2.3 mg cm^{-2} surface area of retina.

INTRODUCTION

The eye of the ladyfish *Elops saurus* has a conspicuous reflector or tapetum lucidum, which contains white reflecting material. The outer retina is organized like that of mooneyes (*Hiodon*). It is a grouped retina, *i.e.* the photoreceptors are organized in bundles, separated by wedge-shaped processes of pigment epithelial cells. In the photopic eye, grouped cones lie against the external limiting membrane, and rods are displaced distally between processes of the pigment epithelial cells. Granules of melanin pigment are aggregated into the distal tips of the cell processes. The tapetum is retinal *i.e.*, it occupies the pigment cell processes, and is duplex in nature. A multitude of reflecting particles extends throughout most of the length of the cell, forming a diffusely reflecting tapetum, whereas some kind of orderly array of reflecting crystals forms a sheath about the cones (McEwan 1938, Wagner and Ali 1978, Best and Nicol 1979). In this paper we show that the reflecting material of the tapetum of *Elops* is guanine.

MATERIALS AND METHODS

One fish of 29 cm length was used for chemical studies. The eye was 12.8 mm wide and 11.7 mm high. The retina and pigment epithelium from one eye were collected together; they were homogenized with a little water in a Ten-Broeck tissue-grinder and centrifuged. The pellet was extracted with 1M HCl (4 ml) for 1 h at room temperature and centrifuged. The extract was chromatographed ascendingly on Whatman No. 1 paper together with standards, guanine, adenine, hypoxanthine, xanthine, and guanosine. Solvent systems used were: methonal-conc. HCl-water (7:2:1), 1-propanol-1M HCl (3:2), and 1-propanol-conc. NH_4OH-water (6:3:1) (v/v or v/v/v).

Guanine was isolated from the 1M HCl extract; a half volume of this was adjusted to pH 5 with 1M NaOH. A precipitate formed immediately. It was kept at 2°C overnight, the powder was collected by centrifugation, washed with water, and then dried at 40°C in a vacuum oven. It weighed 4.0 mg.

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The other eye of the specimen was extracted with 0.1M NaOH (10 ml) at room temperature for 30 min. The extract was cleared by centrifugation and an aliquot was used to quantify guanine by the method of Nicol and Van Baalen (1968).

U.v. absorption spectra were recorded on a Beckman spectrophotometer model 24; i.r. absorption spectra on a Perkin-Elmer i.r. spectrophotometer model 237B.

RESULTS

The chromatograms of the 1M HCl extract from the retina and pigment epithelium showed one very intense spot detected under a u.v. lamp (254 nm). It moved at the same rate as guanine. The u.v. spectra at pH 1 and 13 of the isolated powder were superimposable on those of guanine. Furthermore, the i.r. spectrum of the powder taken in a KBr pellet resembled very closely that of guanine (Fig. 1). The tapetum of an eye contained 8.6 mg of guanine. There were approximately 2.3 mg cm^{-2} retinal surface.

When a large quantity of the 1M HCl extract was chromatographed in the

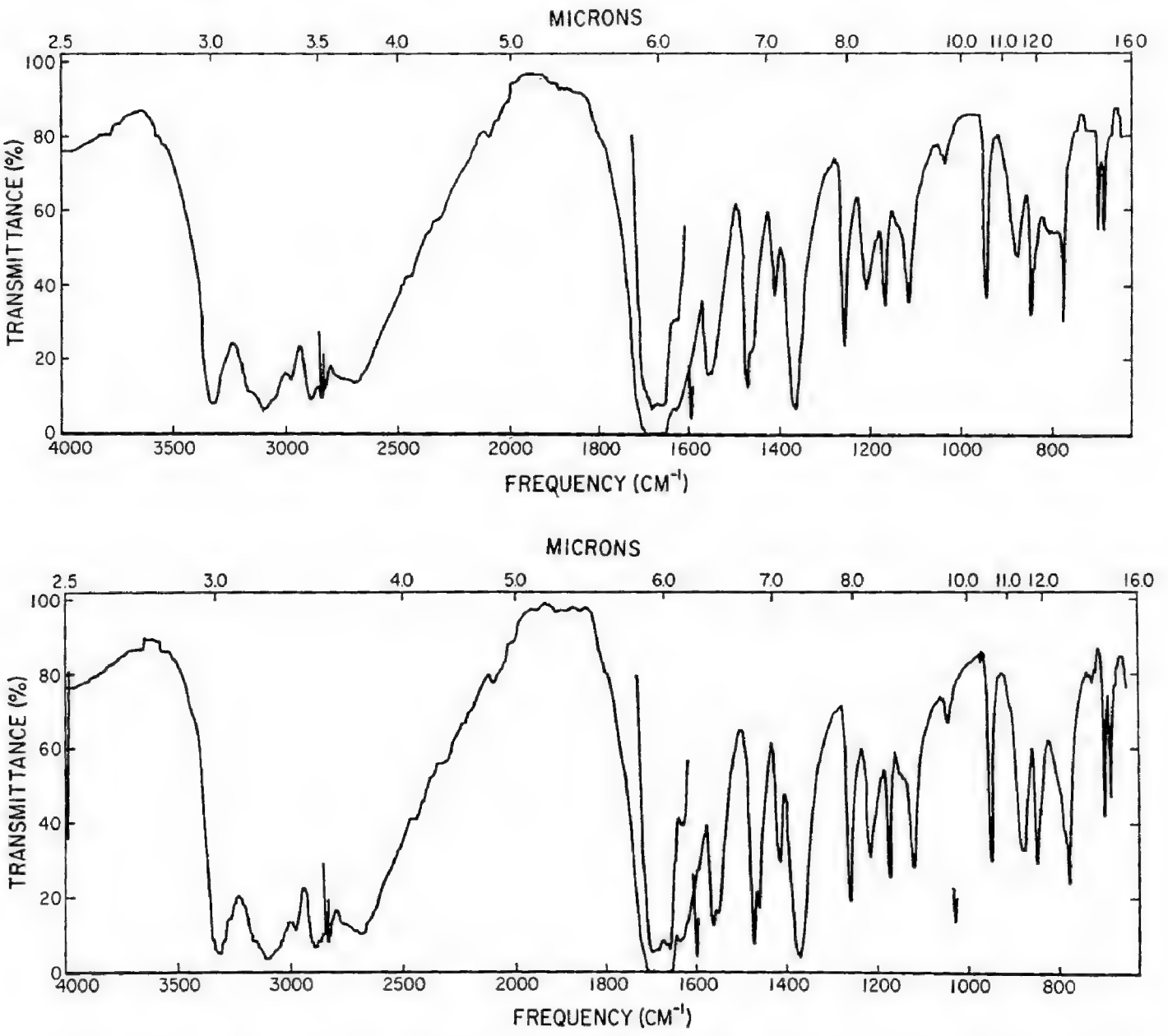

FIG. 1. Infra red spectra of reflecting material from the tapetum of the ladyfish (above), and of authentic guanine (below). Quantities examined were 0.95 mg of tapetal material or of guanine in 150 mg K Br.

solvent propanol-NH_3, a faint spot was detected which corresponded to hypoxanthine. Therefore, quantification was carried out for the ratio of guanine to hypoxanthine. On Whatman No. 3 MM paper, 50 ml of the 1M HCl extract was applied along with 100 μg of guanine and 1 μg of hypoxanthine. The paper was developed in 1-propanol-conc. NH_4OH-water (6:3:1) for *ca.* 10 h. The materials were extracted with adequate volumes of 0.1M HCl and the extracts were analyzed by spectrophotometry. The guanine to hypoxanthine ratio in the HCl extract was 100:0.7.

REMARKS

The reflecting material in the retinal tapetum lucidum of the ladyfish is guanine in crystalline form, together with a very small proportion of hypoxanthine. Guanine crystals from fish skin also contain some hypoxanthine (Greenstein 1966). The quantity of guanine is 4 $\times$ greater than in the retinal tapetum of the anchovy and the choroidal tapeta of selachians (Nicol and Van Baalen 1968, Zyznar and Nicol 1973). Guanine, as a reflecting material, was first discovered in the retinal tapetum lucidum of the ruff *Acerina* (Kühne and Sewall 1880), and has also been identified in retinal tapeta of several deep-sea fishes (Zyznar *et al.* 1978, Somiya 1980). Other kinds of crystalline reflecting materials found in retinal tapeta lucida of fishes (but not *Elops*) are 3,4-dihydroxanthopterin in shad *Dorosoma* and pike-perch *Stizostedion*, and uric acid in mooneyes *Hiodon* (Zyznar and Nicol 1973, Zyznar and Ali 1975, Wagner and Ali 1978, Zyznar *et al.* 1978). These three crystalline substances have high refractive indices, which make them efficient reflectors in systems composed of thin films or small particles that achieve reflection through constructive interference or backscattering of light. The majority of fish retinal tapeta lucida contain still other kinds of reflecting materials, namely lipid (a triglyceride) or catfish reflecting material (a polymerized indole + decarboxylated S-adenosylmethionine) (Zyznar and Nicol 1973, Ito *et al.* 1975). The organization of the outer retina of the ladyfish is imperfectly known; it shows many features parallel to those of mooneyes *Hiodon*, with guanine occupying the reflecting role of uric acid. *Elops*, like *Hiodon* and some deep-sea fishes, has a retina in which the receptors (rods and cones, rods only in deep-sea species) are arranged in tight groups, each surrounded by a sheath of reflector and pigment, and separate from its neighbours. The receptors in each group are apparently optically coupled, and there is a high degree of vertical summation (Locket 1977, Wagner and Ali 1978). The eye of *Elops* presents many unusually interesting features and presents an opportunity to study the visual role of a grouped retina by electron microscopy, electrophysiology and photometry.

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BIOLOGICAL NOTES ON THE SHARKS OF THE NORTH CENTRAL GULF OF MEXICO[1]

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ABSTRACT

From January 1978 through February 1980, 621 sharks of 18 species were examined or tagged in the north central Gulf of Mexico between the mouth of the Mississippi River and Cape San Blas, Florida, and offshore to waters 2000 m deep. The majority of sharks were caught on floating longlines. Specimens were taken in all months of the year, but many species were caught more frequently in October and November. The numbers of females were about twice those of males in all species except *Sphyrna lewini* where males greatly outnumbered females.

Most species had a fairly widespread distribution, but *Carcharhinus brevipinna* was taken primarily west of Mobile Bay and *C. plumbeus* occurred more commonly east of there. For most species, males mature at a smaller size than females, and do not attain as great a length. *Rhizoprionodon terraenovae*, *Carcharhinus acronotus*, *C. brevipinna*, and *C. limbatus* were taken in sufficient quantities to determine their reproductive cycles. All four species have a breeding period in June and July, a gestation period of 10–12 months, and a parturition period from late April or early May through early June. The limited reproductive data for the remaining species tended to follow a similar trend, except possibly for *Galeocerdo cuvieri* and *Carcharhinus obscurus*.

A range extension for *C. signatus* was established with one specimen taken near the surface over 2000 m of water at 28°58′N 87°33′W.

INTRODUCTION

Shark surveys along the Gulf coast of the United States are restricted primarily to southern Florida and Texas. Springer (1938) noted the paucity of records for Gulf sharks in his account for the Florida east and west coasts, and stated that much additional research was necessary. Bigelow and Schroeder (1948) summarized the systematic and biological literature on the sharks of the western North Atlantic, including the Gulf of Mexico. Their biological data however, were often limited, and their Gulf records depended largely on Springer's knowledge of the Florida area. The first synopis of the sharks of the western Gulf (Baughman and Springer 1950) included 23 species found or expected along the Texas coast. Clark and von Schmidt (1965) reported on 23 species of sharks found along the central Florida Gulf coast, and provided excellent life

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history information for 13 of them. No shark surveys have been published specifically concerning the northern Gulf of Mexico, but two recent keys (Hoese and Moore 1977, Boschung 1979) indicate the species likely to occur in the north central portion of the Gulf.

No one study contains the data necessary for a definitive publication on the sharks of the Gulf of Mexico, yet each report adds information leading towards this end. The Gulf of Mexico Fishery Management Council (GMFMC) (1979) prepared a management plan for a shark fishery in the Gulf of Mexico, but this plan is based on incomplete life history knowledge and unknown species-stock composition. The words "insufficient information" recur throughout the GMFMC draft. The GMFMC manuscript states "Probably the greatest concentrations of sharks in the Gulf occur during the summer in the north central area near the mouth of the Mississippi River." The goal of this report is to increase the data on the biology and distribution of the species of sharks found in this north central region.

METHODS AND MATERIALS

This survey, conducted from January 1978 through February 1980, included the marine waters from Cape San Blas, Florida west to the mouth of the Mississippi River, and out to the 2000 m curve of the DeSoto Canyon.

Small numbers of sharks were captured in trawls, gill nets, and seines. The major fishing tournaments (rodeos) held along the Gulf coast each summer have a general category for sharks, and the entries in several rodeos were examined. Of any tournament, the Biggs Pensacola Shark Rodeo offered the greatest opportunity to examine the species discussed here. Floating longlines were used to collect the majority of specimens. Sixty-nine sets, totalling 6476 hooks, were fished in waters 10 to 2000 m in depth (Fig. 1). Hooks were fished from near the surface to the bottom, or, when over deep waters, to a maximum of 80 m. Small- and medium-sized species were collected on longlines throughout the study, but the large species were caught only after gangion modifications ten months prior to the end of the study. Rod and reel fishing supplied many of the smaller species, and was conducted in conjunction with the longline cruises. In addition, many days were spent rod and reel fishing near Dauphin Island, Alabama. Local boat and beach sport fishermen also contributed several specimens.

Specimens collected by me that appeared in good physical condition were tagged and released after sex and total length were determined. Many of these lengths were estimated as no method was available for handling of sharks that exceeded 125 cm TL in confined quarters. Specimens not tagged and released were weighed (if possible), up to 42 morphometric measurements were taken, representative jaws and all embryos were kept, gonads were examined for development and any other pertinent data (parasites, injuries, etc.) were recorded.

Sexual maturity was determined by the methods of Springer (1960) and Clark and von Schmidt (1965). Males were considered mature if the claspers were well calcified, could be rotated forward easily, and the rhipidion (head) of the clasper spread fully and easily. Fully developed siphon sacs were also used as a criterion. Examinations during this survey showed that siphon sacs develop rapidly with the onset of puberty. Claspers were often considered mature yet siphon sacs would be only partially developed. Specimens in this condition were considered late adolescents or sub-adults. Clark and von Schmidt (1965) found sperm present in males with immature claspers; therefore, the presence of sperm in the seminal vesicles cannot be used for a criterion of maturity.

Females were considered mature if the hymen covering the distal portion of the oviducts was ruptured, the ovary contained developing eggs, the uteri were expanded and sac-like (not constricted and tubular), or if eggs or embryos were found in the uteri.

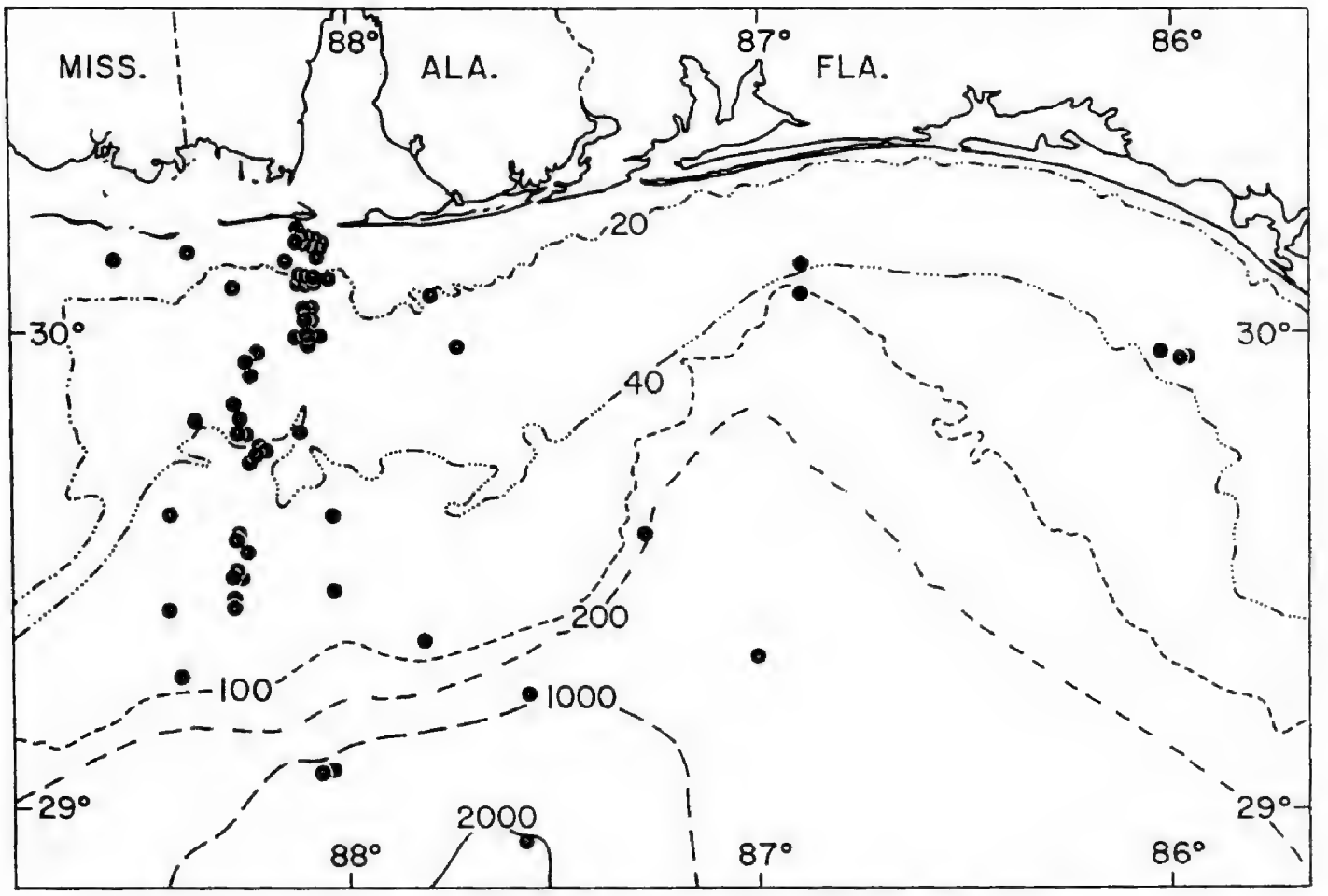

FIG. 1. Location of the 69 longline sets from March 1978 through February 1980. Depth contours in m.

Males with large amounts of sperm in the seminal vesicles, enlarged testes, and a white mucous in the clasper grooves indicated the mating season. Females were considered in mating condition when large mature ovarian eggs were present, or if fresh, often crescent-shaped bite wounds inflicted during mating (Stevens 1974) were present. Sperm in smears from the vagina and uterus are excellent indications that mating has occurred, but this measure was not attempted as most examinations occurred at sea where time and conditions were not always favorable for the preparation and examination of smears.

Embryos were carefully removed from the uteri. Notes were taken on the location of embryos within the uteri, and whether or not yolk-sac placentae were present and attached to the uterine walls. Sex of the embryos, determined by the presence or absence of claspers, was apparent within the first two months of gestation, and was recorded along with total lengths of the embryos and lengths of the umbilicals.

Total lengths are used throughout this report. Total lengths for mutilated specimens were estimated from what proportional measurements were available. Scientific names follow Compagno (1978). Bigelow and Schroeder (1948), Baughman and Springer (1950), and Clark and von Schmidt (1965) offer good bibliographies of the historical literature on each species and, therefore, this type of review is omitted from this report.

GENERAL RESULTS

This report is based upon data taken from 621 sharks of 18 species (Table 1). The small- and medium-sized species (less than 250 cm) are represented in most size ranges, whereas the larger species are represented primarily from rodeo entries, and therefore include few juveniles. Most species were sexually dimorphic with males smaller than females, but due to incomplete tag records

TABLE 1

A summary of the number and size range of sharks examined and tagged during the survey, January 1978 through February 1980. Species are listed by decreasing total number collected. Measurement ranges in cm TL.

Species	Sharks Examined			Sharks Tagged[1]			Total
	Males	Females	Incomplete information[2]	Males	Females	Incomplete information[3]	
	No. (Size Range)	No. (Size Range)	No. (Size Range)	No. (Size Range)	No. (Size Range)	No. (Size Range)	
Rhizoprionodon terraenovae Atlantic sharpnose shark	16(54-107)	62(67-107)	44(80-110)	4(85-96)	26(86-105)	22(85-100)	174
Carcharhinus limbatus Blacktip shark	42(52-160)	75(94-178)	1(135)	14(110-155)	17(90-160)	7(100-155)	156
Carcharhinus leucas Bull shark	15(84-229)	32(141-266)	------	------	1(230)	------	48
Galeocerdo cuvieri Tiger shark	5(200-305)	8(106-410)	2(200)	2(213-290)	14(107-260)	14(137-230)	45
Carcharhinus acronotus Blacknose shark	5(105-122)	12(53-126)	4(100-120)	6(100-130)	2(105-107)	8(85-120)	37
Carcharhinus brevipinna Spinner shark	7(97-181)	27(68-225)	------	------	------	------	34
Carcharhinus plumbeus Sandbar shark	4(179-205)	16(97-215)	------	2(180)	12(180-215)	------	34
Sphyrna lewini Scalloped hammerhead shark	18(197-254)	2(150-204)	------	7(137-260)	4(213-300)	3(153-230)	34
Carcharhinus obscurus Dusky shark	7(287-308)	8(245-335)	------	------	2(190-200)	------	17
Carcharhinus falciformis Silky shark	4(89-190)	2(82-96)	------	------	------	11(75-96)	17
Sphyrna mokarran Great hammerhead shark	2(176-188)	6(222-318)	1(150)	------	1(183)	------	10
Carcharhinus isodon Finetooth shark	2(112-120)	2(127-139)	------	1(127)	------	------	5
Isurus oxyrhinchus Shortfin mako shark	4(175-218)	1(300)	------	------	------	------	5
Carcharhinus signatus night shark	------	------	------	------	1(190)	------	1
Negaprion brevirostris Lemon shark	1(235)	------	------	------	------	------	1
Eugomphodus taurus Sand tiger shark	------	1(145)	------	------	------	------	1
Alopias vulpinus Thresher shark	------	1(156)	------	------	------	------	1
Sphyrna tiburo Bonnethead shark	------	1(51)	------	------	------	------	1
							621

1 Many tag measurements are estimates.
2 This column includes incomplete data sheets or sharks that had been mutilated on the longlines.
3 This column includes tagged sharks in which lengths and sex were recorded, but the sex records were made only on the cards sent to the National Marine Fisheries Service, Narragansett, Rhode Island.

(see footnote 3, Table 1) a separation of sexes is not attempted when presenting length-frequency data (Fig. 2).

No general analysis of seasonal distribution has been attempted as specimens were taken by several methods, and rodeo data would tend to bias results, but seasonal analysis is included separately for several species.

Four species (*Rhizoprionodon terraenovae*, *Carcharhinus acronotus*, *C. brevipinna*, and *C. limbatus*) were examined in sufficient quantities or seasons to determine mating, gestation, and parturition times. These data indicated a mating period from late June through early July, a gestation period of 10–12 months, and parturition from early May through early June. Clark and von Schmidt (1965) suggest a longer (12–16 month) gestation period for large species such as *Galeocerdo cuvieri* and *C. obscurus*.

Embryonic development for the carcharhinids I examined was very similar. Early in the gestation period (July and August), embryos are distributed throughout the length of each uterus, and the most posterior embryo is the

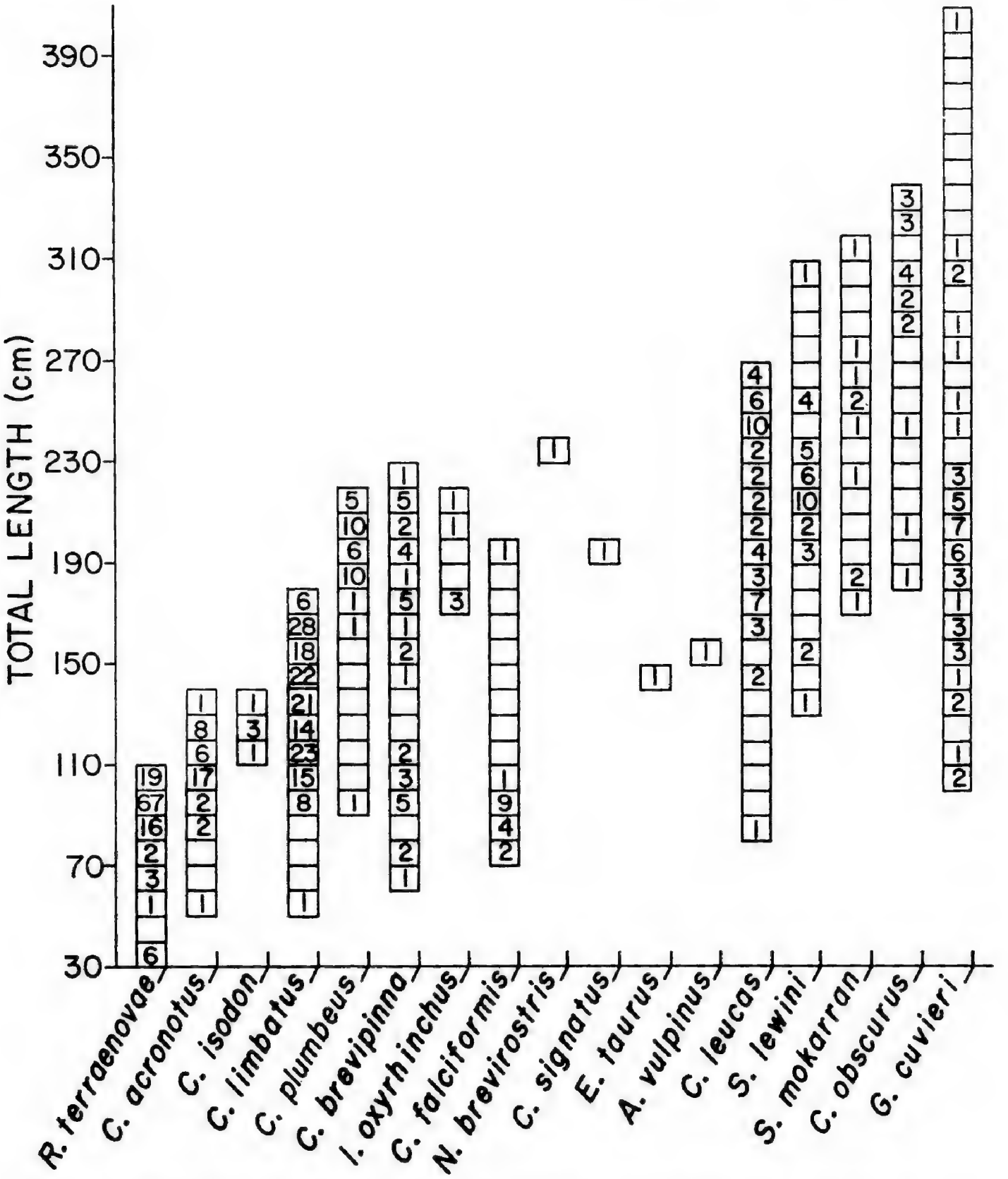

FIG. 2. Length-frequency distribution of 17 species of sharks examined. Sixty-six sub-adult and adult *R. terraenovae* are excluded due to no exact record of their length.

largest. Embryos decrease in length the more anteriorly they are located, and often an undeveloped egg or eggs will be the most anterior. Both uteri have similar sized embryos which suggest that two eggs ovulate at approximately the same time and pass one to each oviduct. This process is apparently repeated several times until some mechanism (presumably hormonal) stops ovulation. Although the embryos measure to within 1.0–1.5 cm of each other at this early stage of development, the differences in physical development are readily ap-

parent. By the time embryos reach mid-term, they are positioned side-by-side with their heads oriented anteriorly, and all are approximately the same length. Each embryo is enclosed in a longitudinally oriented membranous chamber formed from the uterine wall. The yolk-sac placentae are formed by October, and are attached to the posterior portion of the uterine wall by November. Gilbert and Schlernitzauer (1965, 1966), and Schlernitzauer and Gilbert (1966) describe the uterus and placentation of *Carcharhinus falciformis* and *Sphyrna tiburo* in detail, and no differences were noted in any of the specimens examined here. When full-term, embryos occupy the entire expanded uterine cavity, and are born tail first. Wass (1973) gives an excellent description of the birth of a *Carcharhinus plumbeus* pup.

Apparently, most carcharhinid females do not immediately breed again following parturition. There is at least one non-gravid year in the reproductive cycle in which ovarian eggs develop, and the female rebuilds depleted food reserves which nourish the developing embryos. Backus, *et al.* (1956), Springer (1960), Clark and von Schmidt (1965), Wass (1973), and Dodrill (1977) recorded significant numbers of adult non-gravid females. These authors suggest that there may be at least two non-gravid years (for some species) between gravid periods.

Longlining yielded 381 sharks of 15 species, and 22 teleosts of eight species (Table 2). Catch-per-unit-effort (Table 3) was biased by the time of day that lines were set, with fewer returns occurring during mid-day, and increased catches occurring during crepuscular periods.

Several specimens of three species (*Carcharhinus acronotus*, immature *C. limbatus*, and *Rhizoprionodon terraenovae*) were attacked and devoured while on longlines. The width of the toothmarks and the curvature of the usually clean bites indicated that the attacking sharks were large. *Carcharhinus leucas*, *C. obscurus*, or *Galeocerdo cuvieri* could have been the attackers; all three of these species are reported to feed on small sharks.

SPECIES ACCOUNTS

Family ODONTASPIDIDAE

Eugomphodus taurus (sand tiger shark)—One specimen, a 145 cm immature female, was collected on longline 13 March 1978. A second female of similar length was seen at the 1978 Pascagoula Fishing Rodeo, but was unavailable for examination. The Dauphin Island Sea Lab has a set of jaws from a 320 cm specimen collected off Dauphin Island in the summer of 1973. Boschung and Couch (1962) reported the capture of a male sand tiger shark (*ca.* 150 cm) 13 km south of Santa Rosa Island, Florida.

Family ALOPIIDAE

Alopias superciliosus (bigeye thresher shark)—There are no Gulf records for this pelagic species, although Compagno (1978) included deep Gulf regions outside the continental shelf as areas of possible occurrence.

A thresher shark (approximately 350 cm) captured near the Mississippi Trough off Southwest Pass of the Mississippi River was described to me as having the very large eyes and long pectoral fins characteristic of the species, but no data were available for verification.

TABLE 2

Numbers of fish species examined or tagged from longlines for the study period, March 1978 through February 1980. Species are listed by decreasing total number collected.

Species	Examined	Tagged	Total
Rhizoprionodon terraenovae Atlantic sharpnose shark	87	44	131
Carcharhinus limbatus Blacktip shark	49	36	85
Galeocerdo cuvieri Tiger shark	4	30	34
Carcharhinus acronotus Blacknose shark	18	16	34
Carcharhinus brevipinna Spinner shark	22	0	22
Sphyrna lewini Scalloped hammerhead shark	6	14	20
Carcharhinus plumbeus Sandbar shark	5	14	19
Carcharhinus falciformis Silky shark	2	11	13
Carcharhinus leucas Bull shark	7	1	8
Rachycentron canadum Cobia	6	0	6
Carcharhinus obscurus Dusky shark	3	2	5
Scomberomorus cavalla King mackerel	5	0	5
Coryphaena hippurus Dolphin	4	0	4
Isurus oxyrhinchus Shortfin mako shark	4	0	4
Sphyrna mokarran Great hammerhead shark	1	1	2
Carcharhinus isodon Finetooth shark	1	1	2
Euthynnus alletteratus Little tunny	2	0	2
Lujanus campechanus Red snapper	2	0	2
Megalops atlantica Tarpon	1	0	1
Caranx hippos Crevalle	1	0	1

TABLE 2—Continued

Species	Examined	Tagged	Total
Makaira nigricans Blue marlin	1	0	1
Carcharhinus signatus Night shark	0	1	1
Eugomphodus taurus Sand tiger shark	1	0	1
Total	232	171	403

Alopias vulpinus (thresher shark)—I examined one juvenile female (156 cm) which was caught in a shrimp trawl off the Chandeleur Islands the first week of December, 1979.

Family LAMNIDAE

Isurus oxyrhinchus (shortfin mako shark)—Five specimens, four males and one female, were recorded. The female, not seen, was caught 22 August 1978, on the surface, over waters approximately 200 m deep along the northwestern rim of the DeSoto Canyon, measured approximately 300 cm, weighed 334 kg, and carried 18 pups 25–31 cm in length. Stomach contents included one small shark and the bait (F. Crooke, Pensacola, FL, pers. comm.).

The four males (*ca.* 175, 175, 179, 218 cm) were taken on a longline 12 February 1980, in 40 m of water 40 km south of the west end of Dauphin Island, Alabama.

Family CARCHARHINIDAE

Carcharhinus acronotus (blacknose shark)—This small species, captured in all seasons, was more common from May through mid-November (Fig. 3).

Both males and females reach maturity at lengths of approximately 110 cm. Two males (105 and 107 cm) were late adolescents, a 114 cm male was mature. A female (107 cm) was immature, and another at 110 cm was mature. These lengths are slightly greater than those suggested by Clark and von Schmidt (1965), but agree with Dodrill (1977).

Four gravid females were examined (Table 4). Parturition is estimated to occur in early

TABLE 3

Catch-per-unit-effort of longlines for the different time periods fished and for all longlines fished. Relationship of the number of sharks collected to number of hooks fished for the sixty-nine sets correlated at r=.518 and indicated a CPUE of 5.9 sharks per 100 hooks fished.

Time	Total number of sets	Total number of hooks	Total number of sharks	Mean number of sharks per set	Mean number of hooks per set	Sharks per hook	Hooks per shark
0400–0800	11	1476	100	9.09	134.18	.068	14.76
0600–1000	9	793	23	2.54	88.11	.029	34.48
0800–1200	10	890	38	3.80	89.00	.043	23.42
1000–1400	10	767	29	2.90	76.70	.038	26.45
1200–1600	9	518	27	3.00	57.56	.052	19.19
1300–Dusk	20	2032	164	8.20	101.60	.081	12.39
Overall	69	6476	381	5.52	93.86	.059	17.00

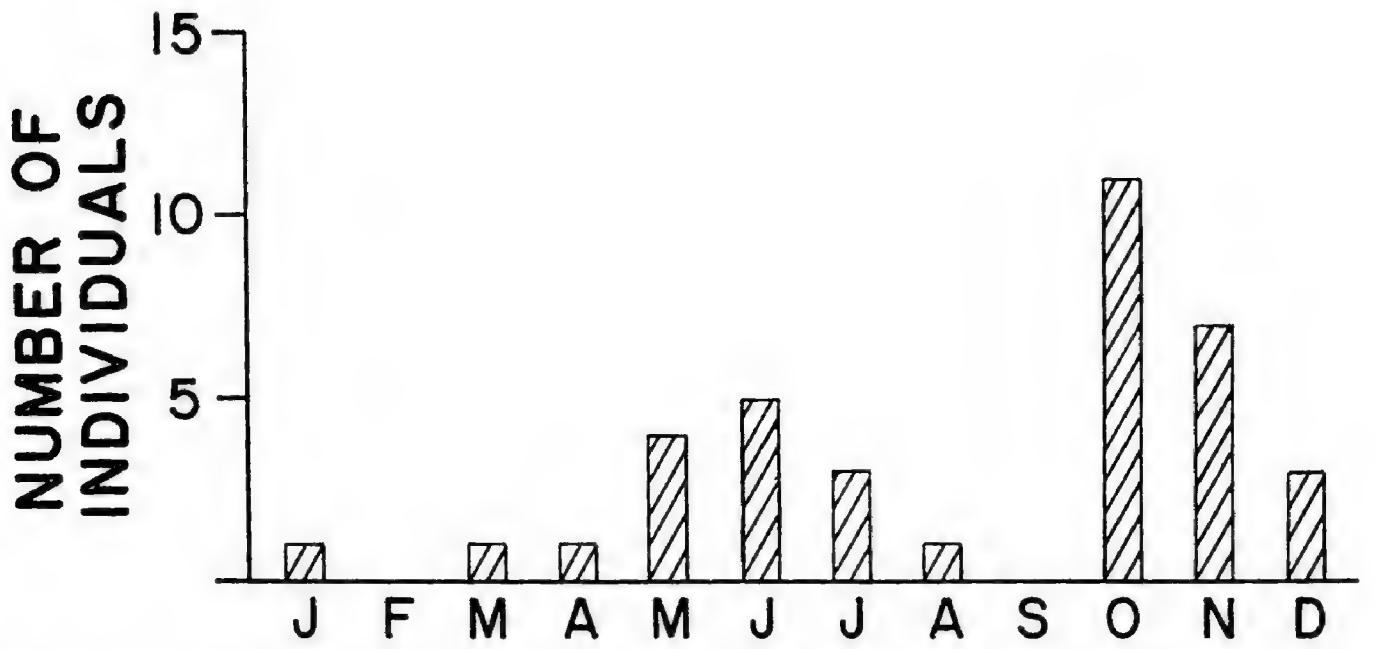

FIG. 3. Catch of *Carcharhinus acronotus* by month. Figure does not indicate CPUE as specimens were taken by various methods.

June with pups born at 45–50 cm. A 53 cm juvenile with a prominent umbilical scar was taken 19 June.

Dodrill (1977) suggested a two year reproductive cycle for *C. acronotus* as he collected both gravid and non-gravid females together off Cape Canaveral, Florida. Although I collected non-gravid and gravid females simultaneously, the near-term females carried large developing ovarian eggs, which suggested they might have bred following parturition.

Weights for specimens above 110 cm varied from seven to eleven kg.

Most stomachs were empty, but food items included an octopus tentacle, and the fishes *Micropogonias undulatus* and *Stenotomus caprinus*. The 53 cm juvenile was caught in a beach seine along with several other juvenile sharks that were actively feeding on schools of anchovies.

The first dorsal fin of a 122 cm female was deformed with the apex folded over and grown to the body of the fin which reduced the height approximately 4 cm.

Carcharhinus brevipinna (spinner shark)—Very little has been reported on the life history of this species in the western North Atlantic, partly due to confusion with the blacktip shark, *C. limbatus*. A detailed discussion of the biology and taxonomic problems of *C. brevipinna* is presented by Branstetter (1980) from specimens collected during this survey.

Thirty-four spinner sharks were examined, and all but three were collected between the mouth of the Mississippi River and Mobile Bay. The others were taken in the vicinity of Pensacola, Florida. Specimens were collected in all months of the year except January and March. Females dominated the catch (Fig. 4).

Females mature at a larger size than males. Two males (171 and 181 cm) were mature, but five females (170.5, 173, 175, 176, 177 cm) were adolescent with little ovarian or uterine

TABLE 4

Data on four gravid *Carcharhinus acronotus* examined.

Female TL (cm)	Date collected	Number of embryos males	females	Range of embryo TL (cm)
113.4	14 July 1979	4 uterine eggs		-------
122.0	05 Nov. 1978	1	3	29.5-30.0
126.0	31 May 1979	4	1	44.5-46.5
122.0	01 June 1979	2	2	44.0-44.5

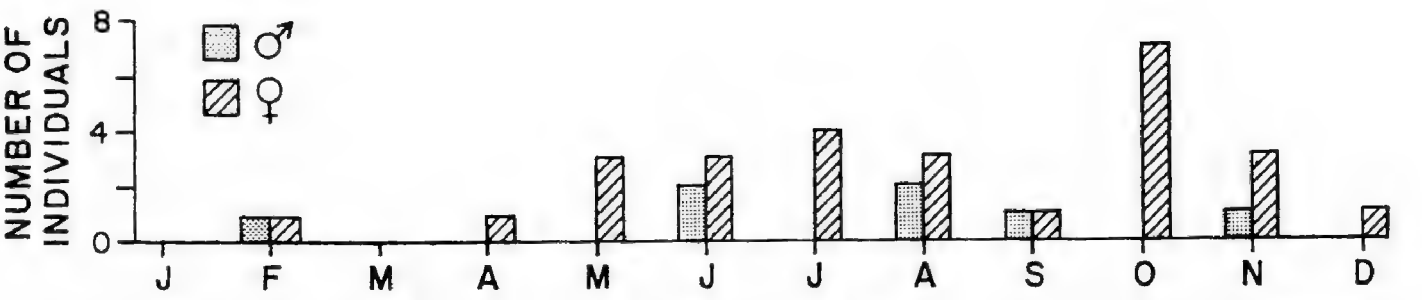

FIG. 4. Catch of *Carcharhinus brevipinna* by month. Figure does not indicate CPUE as specimens were collected by various methods.

development. The smallest gravid female was 191 cm, although two females (192 and 212 cm) were virgin.

The 181 cm male collected 22 June was ripe and the 171 cm male taken 1 August was spent, which suggested a mating season primarily in late June or early July. Seven litters of pups were examined (Fig. 5). Parturition is estimated to occur in late May or early June after an 11–12 month gestation period. The largest embryo measured 64.2 cm, and the smallest free swimming juvenile was 68 cm. Size at birth must range from 60 to 70 cm. The largest recorded litter is 15 pups (Bass, *et al.*, 1973), but these litters averaged seven. Two non-gravid females that had previously carried young were taken in the fall, which suggested a non-gravid year in the reproductive cycle.

A weight-length relationship is shown in Fig. 6.

The remains of two unidentifiable fish were the only stomach contents observed, but all specimens were caught with fresh fish. Spinner sharks were taken at various times of the day, although catches occurred more frequently near dawn and dusk.

The tip of the upper caudal fin of a female apparently had been bitten off just below the notch, and the wound had totally healed.

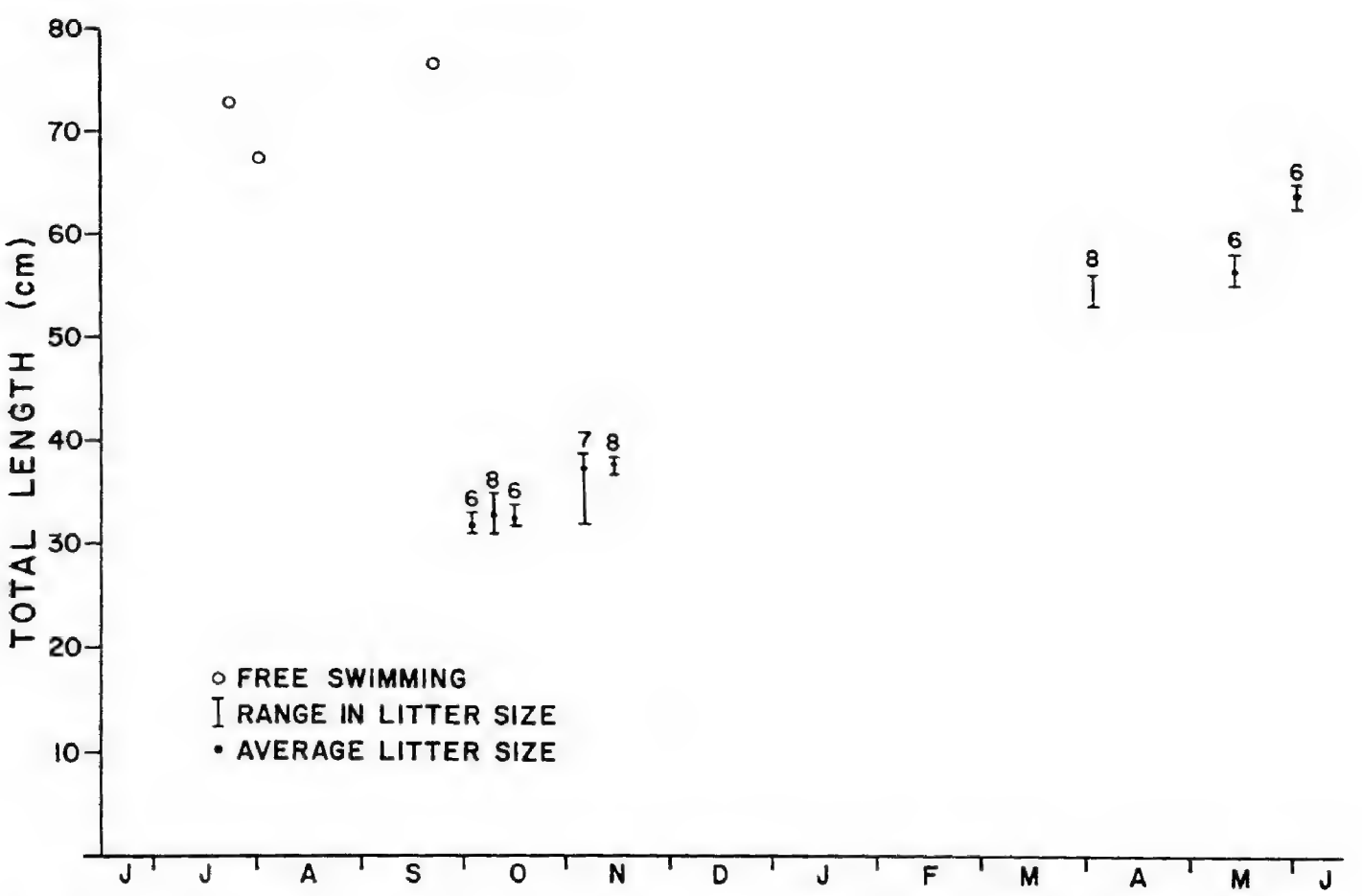

FIG. 5. Monthly size range of *Carcharhinus brevipinna* litters. Numerals above symbols indicate the number of embryos in the litter. April data from Dodrill (1977).

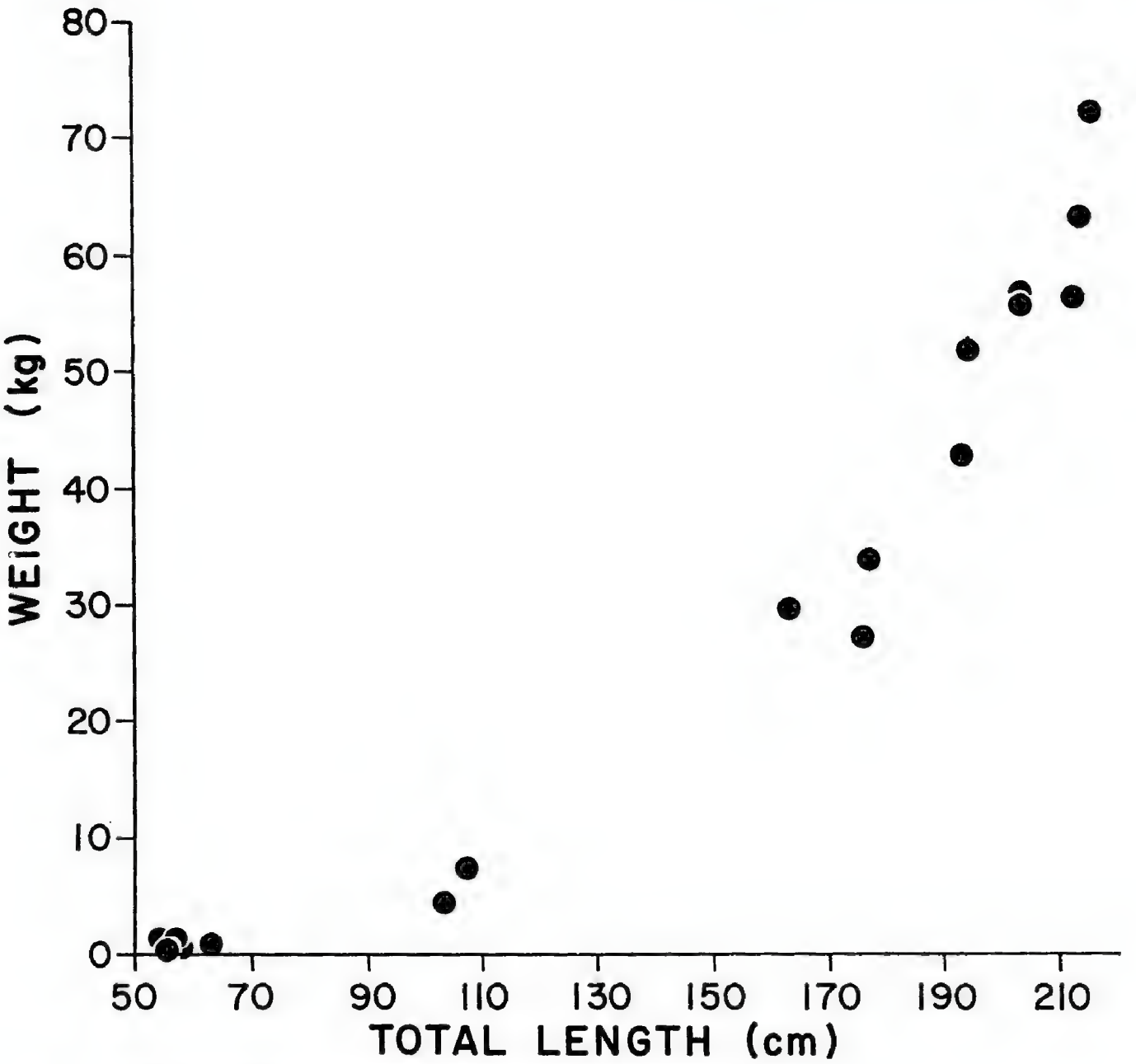

FIG. 6. Weight-length relationship for *Carcharhinus brevipinna*.

Carcharhinus falciformis (silky shark)—This species was represented by 16 juveniles (82.5–109.5 cm) and one sub-adult male (190 cm). The juveniles had a widespread distribution in the study area: two were taken in 36 m of water southwest of Panama City, Florida; two were caught approximately 40 km northeast of the mouth of the Mississippi River in 60 m of water; and 12 were collected along the northern rim of the DeSoto Canyon. Nine of these last 12 were caught on one longline set. This apparent aggregation of juveniles consisted of both sexes. The 38.5-kg sub-adult male was taken near the surface over approximately 1400 m of water 110 km south of Mobile Bay.

Carcharhinus isodon (finetooth shark)—The five specimens collected helped to better define the poorly known life history of this species; they have been previously reported by Branstetter and Shipp (1980). The specimens were collected in June and July near Dauphin Island.

Males mature near 115 cm as a 112 cm male was late adolescent, and two males, 120 and 127 cm, were mature. Females mature at a larger size than males. A 127 cm female was immature, and a 139 cm female collected 5 June carried four full-term pups, 49–51 cm. Moran (1972) reported two gravid females (137 and 142 cm), and four immature females (123, 126, 137, and 142 cm) taken from St. Andrews Bay, Florida. Maturity for females is probably reached at lengths near 140 cm.

Carcharhinus leucas (bull shark)—Only eight of the 48 specimens examined were collected

on longlines. Thirty-eight were entered at either the Dauphin Island or Pensacola rodeos, and beach fishermen caught two off Dauphin Island.

A 212 cm male had calcified claspers (8.9% TL) but the siphon sacs extended anteriorly only 45 cm, or two-thirds the distance to the pectorals. The smallest fully mature male was 217 cm.

The smallest mature female was 228 cm, but two specimens (241 and 242 cm) had not carried young.

No mature males were ripe, and all gravid females were collected in July and August (Table 5); therefore the gestation period could not be determined. Clark and von Schmidt (1965) indicated that *C. leucas* follows the same pattern as other carcharhinids of the area with pups approximately 75 cm in length born in late April and May.

An 84 cm female with a prominent umbilical scar was taken in a gill net at the mouth of Deer River, Mobile Bay, 28 July. Caillouet, *et al.* (1969) collected 38 juvenile bull sharks (mean length 82 cm) from Vermilion Bay, Louisiana, the first two weeks of August. He considered most of them to be young of the year.

Weights increased rapidly with the onset of maturity (Fig. 7).

Stomach contents included the squid *Loligo sp.*, and the fishes *Stenotomus caprinus*, *Diplectrum formosum*, and *Anchoa hepsetus*. Beach fishermen caught one specimen as it fed on a large school of *Brevoortia spp.* Catfish and ray spines were common in the jaws. A tiger shark hooked on rod and reel lost the majority of its abdomen when attacked by another shark, and a large female bull shark caught soon after had portions of fresh shark liver in its stomach.

Many of the gravid females had mating scars and toothmarks across the dorsal surface. The first dorsal fin on one female was folded and fused as in the *C. acronotus* specimen discussed previously; the free tip of her second dorsal fin had been bitten off and had healed.

Carcharhinus limbatus (blacktip shark)—This was the second most common species examined and the most common shark taken near Dauphin Island. Blacktip sharks were taken regularly from February through October (Fig. 8), and were most common in June and July. This ubiquitous species was taken from inside Mobile Bay out to depths of greater than 800 m.

Males mature at a much smaller size than females and do not attain as great a length. Four males (125, 131, 134, 134.5 cm) were late adolescents with developing siphon sacs and/or incompletely calcified claspers. Eight males, 136–160 cm, were mature.

Females smaller than 140 cm showed little reproductive development. Table 6 includes immature females that I assume might have bred during the next mating season. The smallest female that had previously carried young was 158 cm.

June is the primary mating month as four males collected then and in the first week of

TABLE 5

Data on nine gravid *Carcharhinus leucas* examined. The undeveloped eggs in the August record were apparently infertile and had atrophied.

Female TL (cm)	Date collected	Number of embryos	Range of embryo TL (cm)	Number of undeveloped uterine eggs
228	18 July 1979	–	–	6
243	22 July 1978	–	–	5
244	15 July 1979	7	unknown	–
244	23 July 1978	5	5.0–6.0	3
245	23 July 1978	7	4.0–5.5	1
247	21 July 1978	9	3.0–4.5	1
251	21 July 1978	10	3.5–5.0	–
253	21 July 1978	9	3.5–5.5	1
261	26 Aug. 1978	6	12.0–14.5	4

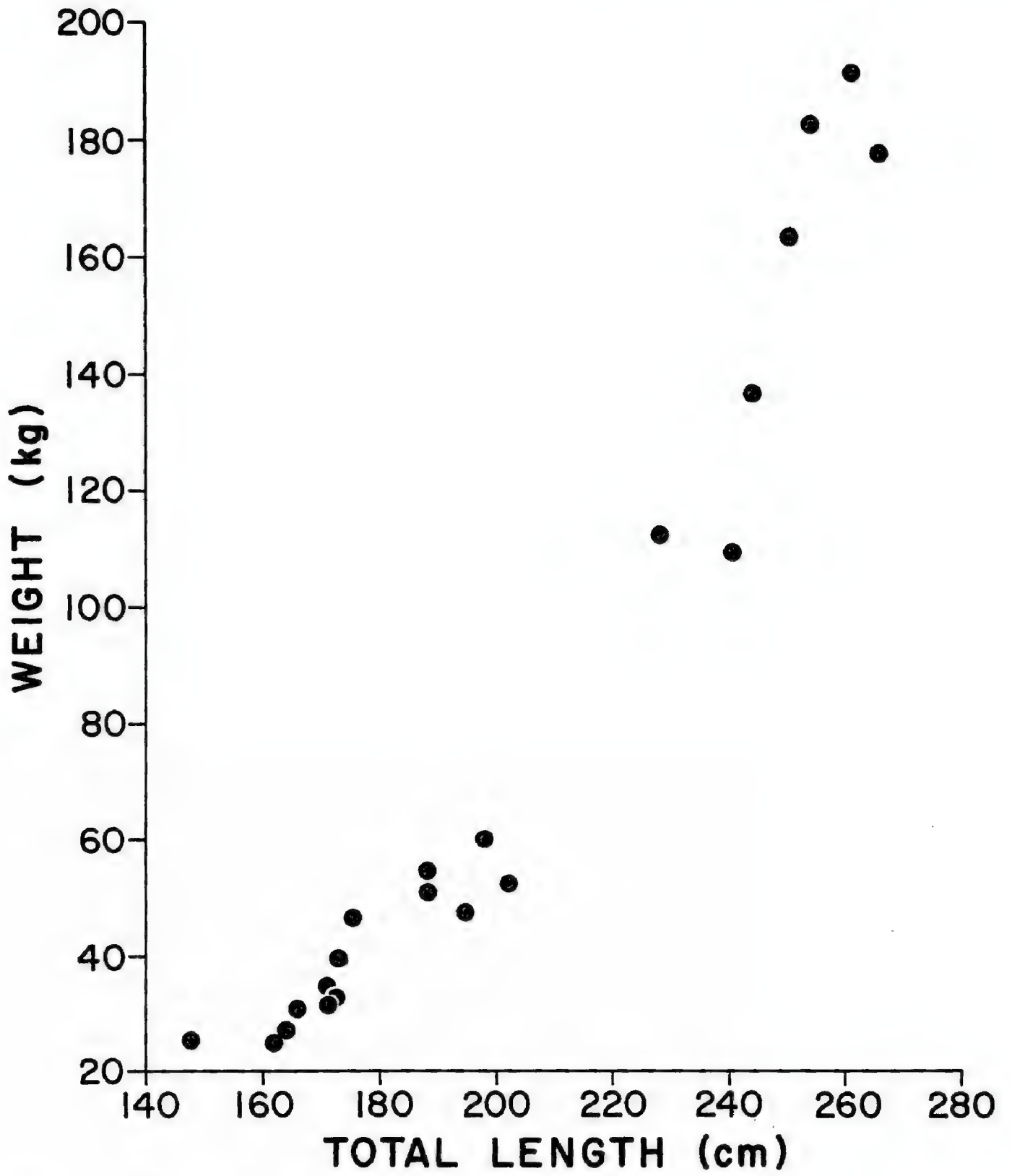

FIG. 7. Weight-length relationship for *Carcharhinus leucas*.

July were ripe, three males taken in late July were spent, and seven females that carried uterine eggs and small embryos were collected in late June and early July.

Seventeen gravid females were examined (Fig. 9), and the gestation period appears to be 11 or 12 months. A female collected 5 June had recently pupped. Her uteri were stretched, flaccid, membranous internally; two placental attachment sites were visible in the posterior portion of each uterus. A second post-partum female examined 21 July had uteri which were in a more contracted state, and not so membranous, but six placental attachment sites were still visible. The largest embryo (61 cm) came from a litter collected in May and a free swimming juvenile (51.7 cm) with an open umbilical slit was taken in early June. Parturition must occur primarily in early June with most litters born at lengths of 50–60 cm. The two

TOTAL LENGTH (cm)	J	F	M	A	M	J	J	A	S	O	N	D
50 – 60						1						
60 – 70												
70 – 80												
80 – 90												
90–100						2	2	1	3			
100–110						2	10	1	1	1		
110–120					2	8	10	1	1	1		
120–130				1	3	3	3	3	1			
130–140		1		2	3	9	2		2	2		
140–150				7	4	5	4	1		1		
150–160		1		5	3	3	4	1	1			
160–170		2		3	4	4	11	2		1	1	
170–180					2	3	1					
Total		**4**		**18**	**21**	**40**	**47**	**10**	**9**	**6**	**1**	

FIG. 8. Seasonal catch for 10 cm size groups of *Carcharhinus limbatus*.

TABLE 6

Development of the reproductive tract for seven immature female *Carcharhinus limbatus* which were expected to breed during the next breeding season. Specimens are listed according to reproductive development in relation to the length of time before the next breeding season.

Female TL (cm)	Date collected	Condition of hymen	Condition of ovary	Condition of uteri
160	01 Aug.	ruptured	little development	tubular
160	13 Oct.	intact	little development	tubular
153	02 Feb.	slight tear	8 eggs 3 cm	tubular
142	17 Apr.	intact	6 eggs 2–3 cm	tubular
159	17 Apr.	intact	7 eggs 3 cm	tubular
160	17 Apr.	intact	8 eggs 3 cm	tubular
151	05 June	intact	6 eggs 2–3 cm	tubular

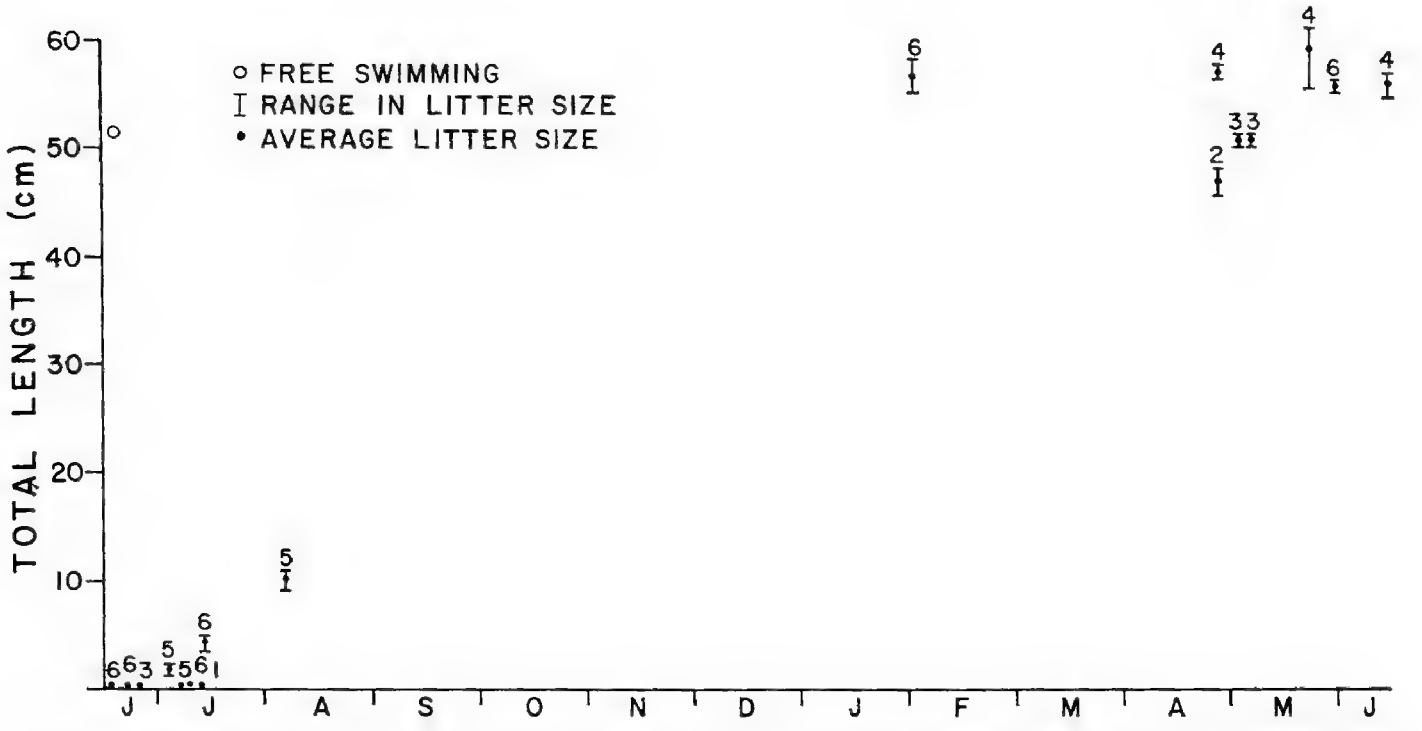

FIG. 9. Monthly size range of *Carcharhinus limbatus* litters. Numerals above symbols indicate the number of embryos in the litter.

post-partum females had no developing ovarian eggs, which suggested a non-gravid year in the reproductive cycle.

Females showed a greater weight increase than males, but gravid females were not significantly heavier than non-gravid females (Fig. 10).

Stomach contents may have been biased by trawl trash as many specimens were taken on rod and reel during trawling operations, but included the fishes *Polydactylus octonemus*, *Anchoa spp.*, a bothid, *Stenotomus carpinus*, *Leiostomus xanthurus*, *Micropogonias undulatus*, *Peprilus burti*, gastropod, a bivalve, and unidentified fish remains. Serrated spines were found in the musculature of several jaws.

Carcharhinus obscurus (dusky shark)—Twelve dusky sharks were entered in either the Dauphin Island or Pensacola rodeos, and five were taken on longlines. This species was taken in both nearshore (inside 30 m depth) and offshore (over depths of greater than 800 m) waters.

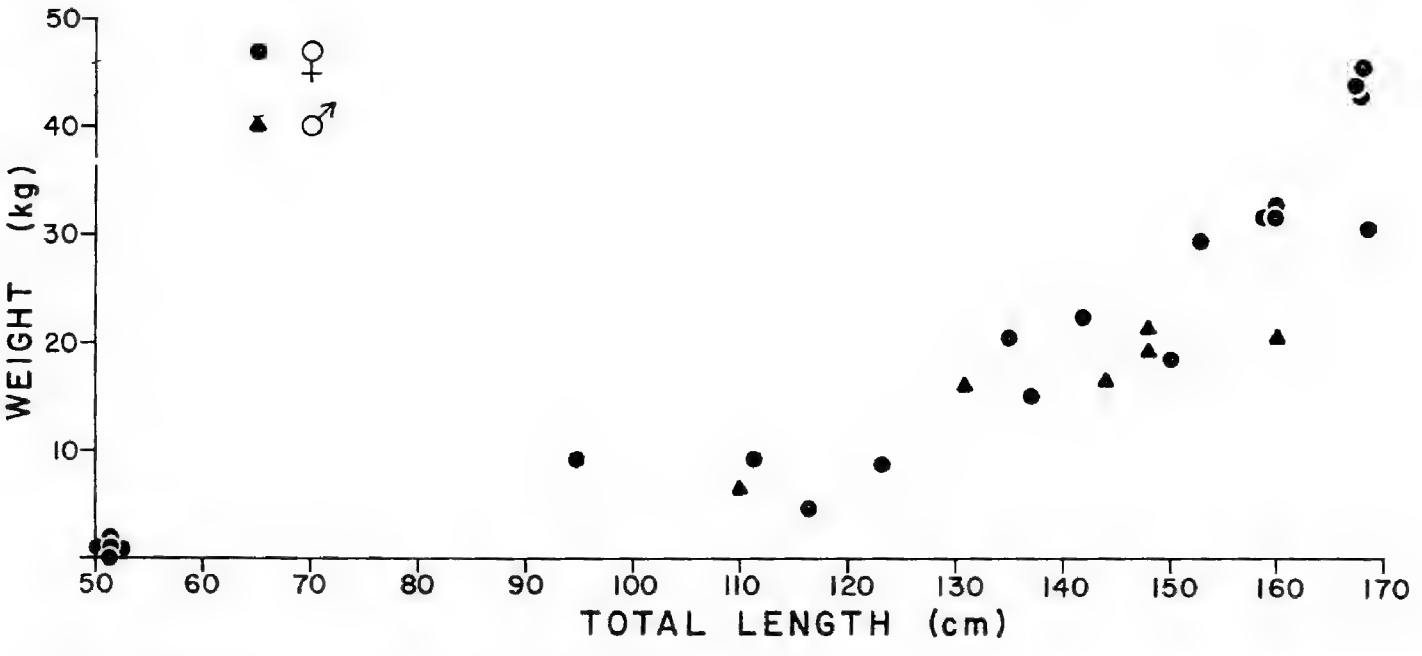

FIG. 10. Weight-length relationship for *Carcharhinus limbatus*.

The smallest mature male (299 cm), collected 18 July, was the only male in mating condition. A 294 cm male had calcified claspers and enlarged testes, but the right siphon sac extended only to mid-belly (44 x 8.5 cm) while the left siphon sac was fully developed (88 x 11 cm).

The smallest mature female (305 cm), examined 21 July 1979, was gravid with 10 near-term embryos (Table 7). A slightly smaller female embryo (77 cm) was taken from a litter of eight on 18 July 1978. Two females, 329 and 326 cm, examined 18 and 21 July, had recently pupped. Eight placental scars were visible in the former, and six were present in the latter. Mating scars were noted in the region of the caudal peduncle and the first dorsal fin of almost all mature females.

A serrated spine had penetrated the esophagus, pericardium, and ventricle of the heart of the 326 cm female listed above. The pericardium was cut in three places from the serrations, and the spine was still rigid external to the heart. Layers of connective tissue, which were forming over the spine both outside and inside the heart, sealed the heart puncture and pericardium. Inside the ventricle the spine was soft and flexible, as if it were dissolving. Apparently, this seemingly serious injury had not greatly affected the shark as it otherwise appeared healthy, and, as noted, had recently carried a litter to term.

Weights varied considerably among individuals. A 244.5 cm female weighed 71.7 kg, and 10 individuals of both sexes, 287–333 cm, averaged 184 kg (range—140.6–220 kg).

As most specimens had everted stomachs, no contents were recorded.

Carcharhinus plumbeus (sandbar shark)—Studies on this species by Springer (1960), Clark and von Schmidt (1965), Bass, *et al.* (1973), and Wass (1973) have resulted in what is probably the best understanding of the life history for any medium sized carcharhinid shark. The records obtained here correlate closely with Springer and with Clark and von Schmidt, but can only be generally associated with Bass, *et al.*, and with Wass because North Atlantic sandbar sharks grow larger than those of other areas of the world.

This species was represented by sub-adults and adults, except for one 97 cm juvenile, and females outnumbered males 28 to six. Sandbar sharks were collected sporadically on longlines from April through December, but most records are from entries in the Pensacola Shark Rodeo. This species prefers a sand-coral bottom habitat (Springer 1960) such as is found north and east of DeSoto Canyon. It was taken more frequently there. Catches between Mobile Bay and the mouth of the Mississippi River were primarily in October and November when turbidity was low. The sub-adults and adults were collected in areas where the water was greater than 30 m deep. The juvenile was taken in the mouth of the Mobile Bay, 25 August.

The claspers of a 179 cm male were 9.5% TL, but were not totally calcified, and the siphon sacs were only partially developed. Records for a 184 cm male state only that the claspers were calcified. A mature 190 cm male captured 18 July had a large quantity of sperm in the seminal vesicles and was considered in breeding condition.

TABLE 7

Length, weight, and sex of eight embryos taken from a 305 cm *Carcharhinus obscurus* collected 21 July 1979.

Right uterus			Left uterus		
TL(cm)	wt.(kg)	sex	TL(cm)	wt.(kg)	sex
82.5	3.2	male	80.0	3.1	female
80.0	2.6	female	84.0	3.1	male
79.0	2.9	male	80.0	2.7	male
81.0	2.9	male	86.0	3.4	female
82.5	2.9	male	81.0	2.9	male

Three females, 182–187 cm, were virgin with little reproductive tract development. The smallest gravid female was 189 cm, but a 203 cm female had not carried young.

Six gravid females were taken from July through early November. Clark and von Schmidt (1965) recorded 23 gravid females from November through early April. Assuming a single Gulf population, I have combined my data and that of Clark and von Schmidt (1965) in Fig. 11 to document closely the gestation period. Two non-gravid females that had previously carried young were collected 11 and 20 November. This supports the conclusions of Springer (1960), Clark and von Schmidt (1965), and Wass (1973) that females must be gravid on only alternating years.

Weights for seven sub-adults and adults are listed in Table 8.

Food items included an octopus tentacle, a xanthid crab, and unidentified fish remains.

Carcharhinus signatus (night shark)—This shark is caught most commonly off the continental shelf (Springer 1950), although Bigelow and Schroeder (1948, 316–319) reported a 93.5 cm

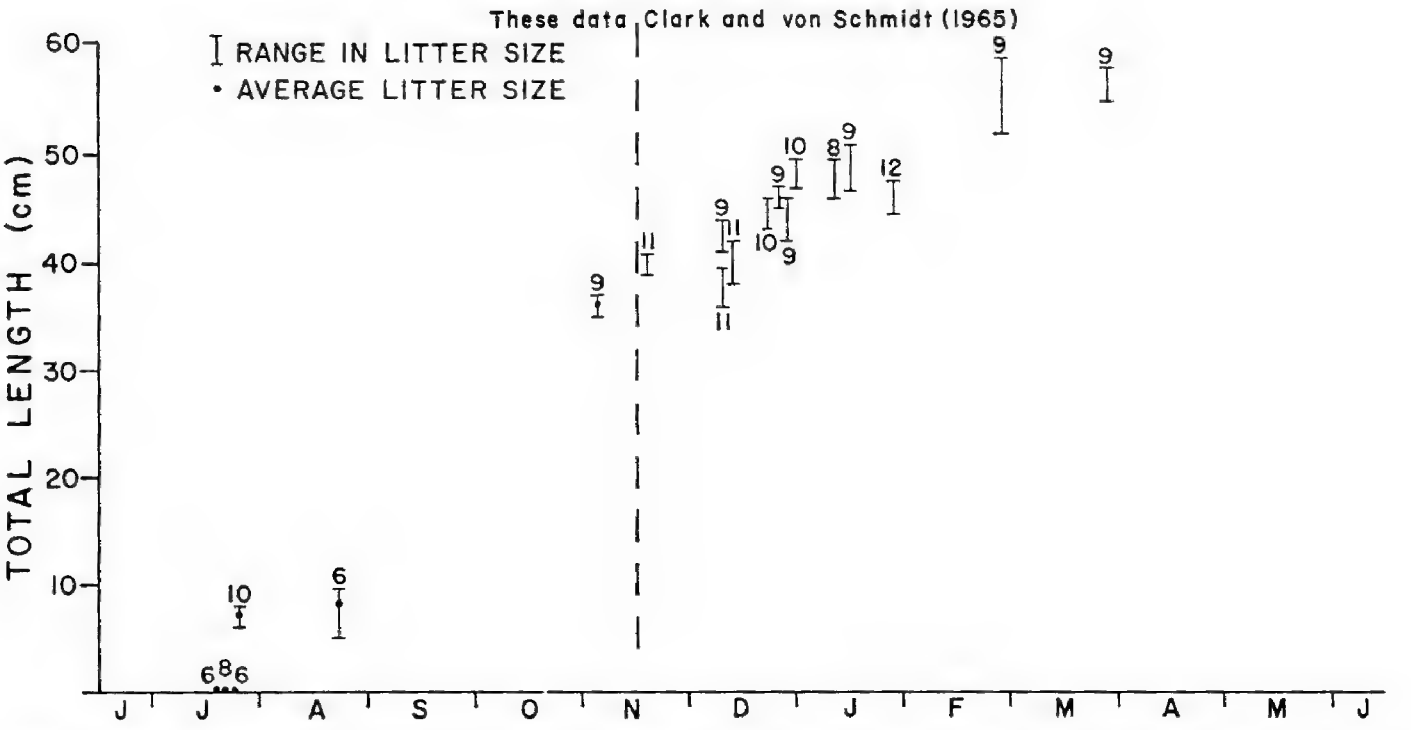

FIG. 11. Monthly size range of *Carcharhinus plumbeus* litters. Numerals above the symbols indicate the number of embryos in the litter. Litters to the left of the hash line are from specimens collected during this study, and litters to the right of the hash line are from Clark and von Schmidt (1965).

TABLE 8

Weight-length relationship for seven *Carcharhinus plumbeus*.

TL(cm)	wt.(kg)
169	29.5
182	36.3
184	34.5
192	44.9
205	51.7
205	69.8
209	61.7

female taken in 28 m of water off South Carolina. Compagno (1978) questioned whether or not *C. signatus* occurs in the Gulf, but Springer and Thompson (1957) reported a 216 cm male taken by trawl 80.5 km east of the Mississippi River at 500 m depth, and Boschung (1979) reported a southeast Gulf capture of a female carrying near-term embryos. B. Rohr (NMFS, Pascagoula, Miss. pers. comm.) reported this female carried 18 pups, and was one of two *C. signatus* taken at 26°34′N 84°50′W. Two of these embryos, a 57 cm female and a 58 cm male (Univ. Ala. Ichth. Coll. 4280), were examined. This record provides a higher number of embryos per litter as Bigelow and Schroeder (1948) and Compagno (1978) reported the number as "up to 12."

One female (*ca.* 190 cm) was taken on an overnight longline set over the 2000 m curve, 25–26 May, at 28°58′N 87°33′W. The shark did not appear to be mature, and after an onboard examination for identification, the specimen was tagged and released.

The large green eyes are indicative of the depths that this species frequents (Springer 1963). Bigelow and Schroeder (1948) and Compagno (1978) indicate most captures are at depths exceeding 200 m. *C. signatus* may move into shallower depths though as the South Carolina record (see above) was inshore, Boschung's (1979) specimen was taken near the surface, the specimen collected here was taken in the upper 80 m of water.

Galeocerdo cuvieri (tiger shark)—The majority of longline catches of this species were juveniles and adolescents; most large individuals were rodeo entries. This is apparently a hardy shark as those individuals taken on longlines were still active after possibly being hooked for as long as five hours. A concentrated effort was made to tag these specimens, especially the smaller juveniles (see Table 1).

Tiger sharks were taken from April through December throughout the continental shelf waters of the study area.

No mature males were examined, but a 305 cm male had partially calcified claspers and developing siphon sacs.

A 317 cm female was adolescent and a 408 cm female was pregnant with 41 pups. Data on these embryos are found in Table 9.

Weights increased rapidly above lengths of 250 cm (Fig. 12).

The only stomach with contents was gorged with approximately 20 liters of what appeared to be trawl trash.

Negaprion brevirostris (lemon shark)—One 235 cm male was examined at the Pensacola Shark Rodeo. These sharks are taken occasionally in summer near Pensacola (F. Crooke, pers. comm.), but I know of only two specimens—one female (268 cm), and one male (272 cm) both caught 12 July 1977—taken from the Mobile Bay area (R. Heard, R. Stiles, pers. comm.).

Rhizoprionodon terraenovae (Atlantic sharpnose shark)—This was the most common shark taken during the survey. Catch per hook on longlines was often as high as 10–20%. Beach fishermen entered such quantities of this species in the Pensacola Rodeo that time did not permit close examination of all entries and records are often incomplete (*i.e.* "17 females, 85–110 cm, gravid with uterine eggs").

TABLE 9

Number and length range of 41 *Galeocerdo cuvieri* pups taken from a 408 cm female caught 22 July 1979.

	Left uterus No. (Range)	Right uterus No. (Range)
Males	7(71–75 cm)	9(74–79 cm)
Females	10(68.3–74.3 cm)	12(72.2–77.1 cm)
Runts	1 egg – 1 pup (15 cm)	2 pups(13.0–16.2 cm)

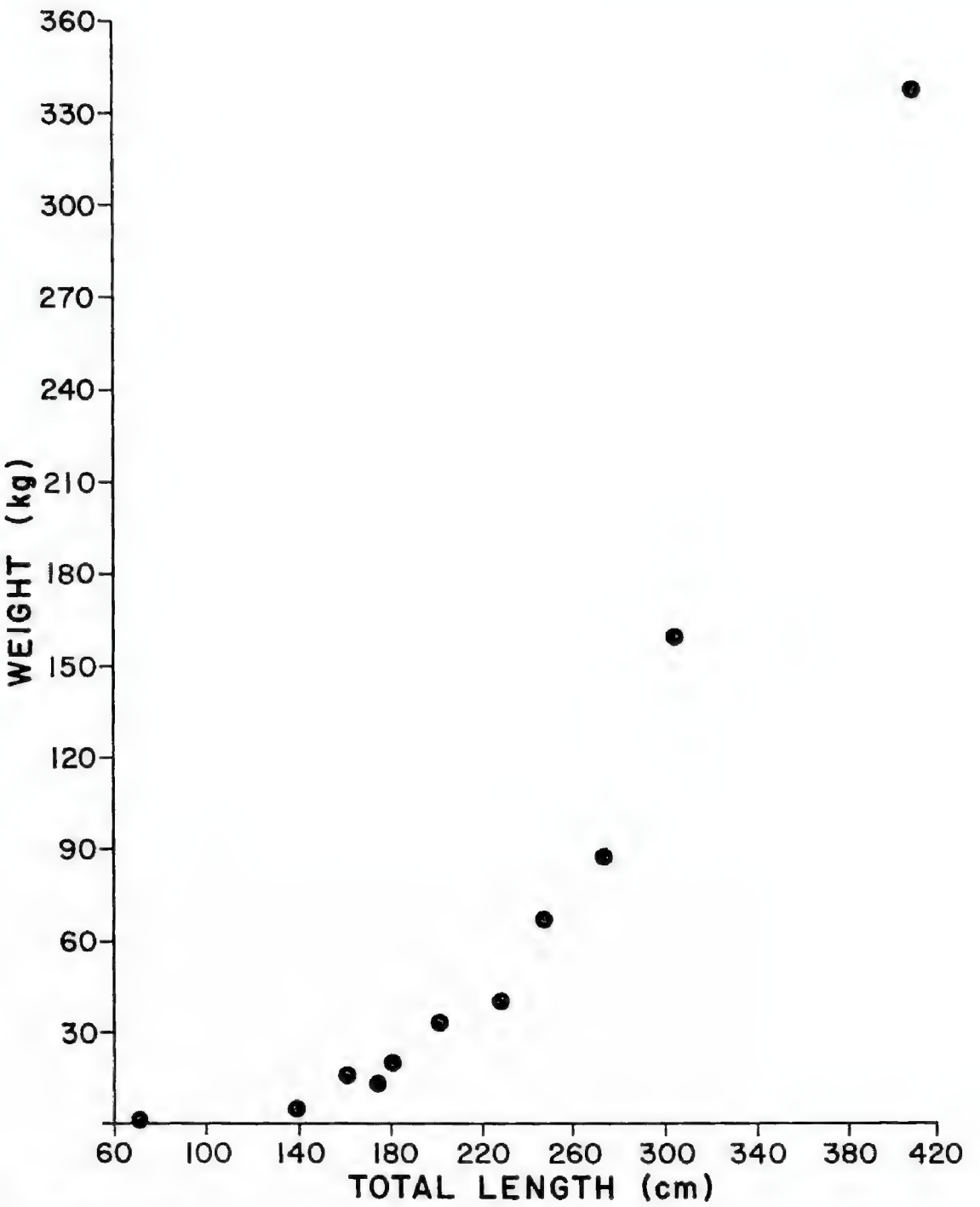

FIG. 12. Weight-length relationship for *Galeocerdo cuvieri.*

Sharpnose sharks were taken throughout the year, except for May and September. Longline catches were predominantly female (ratio near 5:1).

The smallest mature male was 81 cm and the smallest mature female measured 87 cm. The largest male was 107 cm and the largest female was 105 cm.

The gestation period is diagrammed in Fig. 13. The uterine eggs in the August and October records were infertile, and they had atrophied and dried. Free swimming juveniles caught in June bore fresh umbilical scars. May is the estimated time of parturition, and may explain the absence of this species from catch records at this time if females had moved to nursery areas somewhere inshore. Newborn juveniles are commonly taken in shrimp trawls in June and July near Dauphin Island.

All mature females were gravid. The April catches carried large mature ovarian eggs as well as embryos. Apparently, this species breeds each year.

The left ovary is functional in this species instead of the right as is found in other carcharhinids. The umbilicals are covered with long bushy appendicula for absorption of nutrients (Budker 1971).

Food items included unidentified fish remains and the shrimp *Sicyonia sp.*

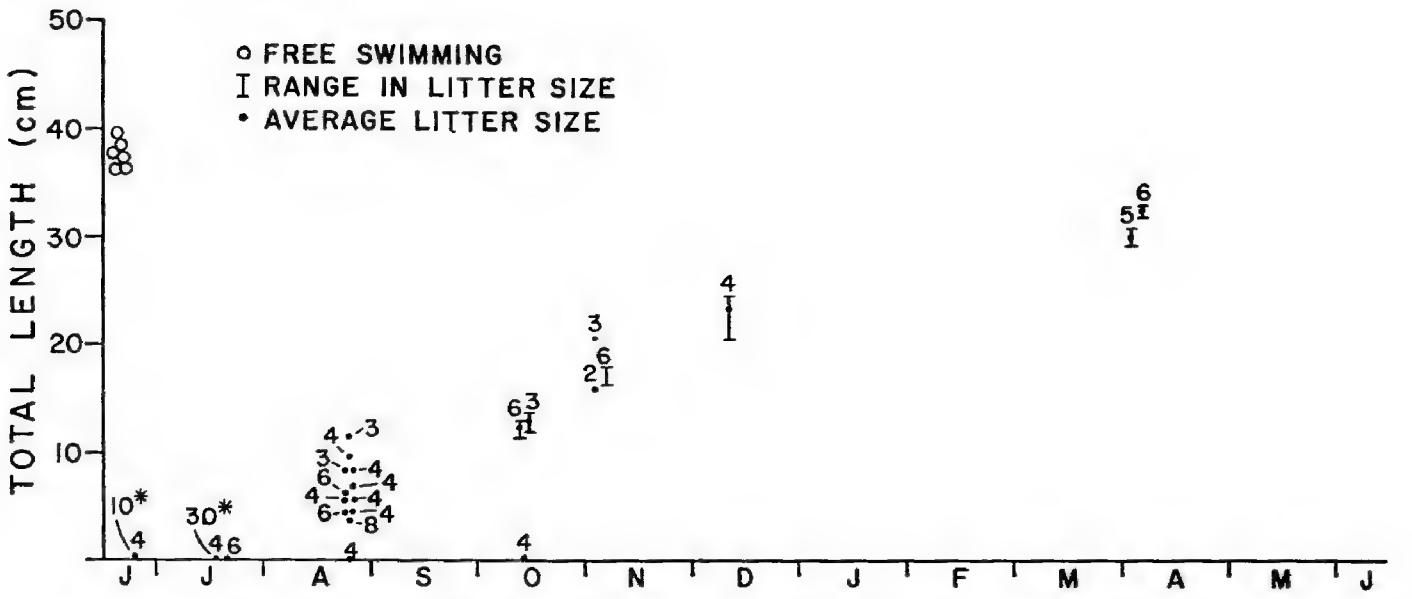

FIG. 13. Monthly size range of *Rhizoprionodon terraenovae* litters. Numerals above symbols indicate the number of embryos in the litter. Numerals with a * indicate the number of litters represented by one data point in the figure. The number above these multi-litter points is the mean number of embryos per litter.

Family SPHYRNIDAE

Sphyrna lewini (scalloped hammerhead shark)—This species was taken sporadically from March through November. Males greatly outnumbered the females. Fourteen of the 34 records are rodeo entries. Usually occurring singly on longlines, five specimens were taken on an overnight longline set 25–26 May, over the 2000 m contour. These two males (250 and 254 cm) and three females (*ca.* 220, *ca.* 220, and *ca.* 300 cm) were the largest specimens recorded.

The two males taken 25 May and one male caught 14 July were in breeding condition. The male taken in July had sperm oozing freely from the claspers.

The smallest mature male was 197.5 cm, and the smallest mature female was 204 cm. No gravid females were examined.

Weights for 10 males 216–233.5 cm varied from 36.3–54.4 kg.

The tip of the upper caudal from just below the notch was missing on two specimens. One male had lost approximately one-half of the upper caudal.

Sphyrna mokarran (great hammerhead shark)—Only two specimens were caught on longlines; one female (*ca.* 180 cm) was tagged just south of Petit Bois Pass, Mississippi in 16 m of water, and the second (*ca.* 250 cm) was taken over the 2000 m curve, but escaped before it could be landed. One specimen (*ca.* 250 cm, sex unknown) was caught on rod and reel and released in the mouth of Mobile Bay in August. The remainder were taken near Pensacola, Florida, in July and entered in the Pensacola Rodeo.

No mature specimens were collected. The largest specimen, a 318 cm female was virgin, although Clark and von Schmidt (1965) recorded a gravid 304 cm specimen.

A weight-length relationship is given in Table 10.

Sphyrna tiburo (bonnethead shark)—One juvenile female (51 cm) was taken in Mississippi Sound near Dauphin Island. The absence of this reportedly common species from catch records is unexplained. Longlines were fished in areas this species should frequent. The size of the longline gear is not thought to have selected against this small shark because Atlantic sharpnose sharks were easily caught.

It is possible that the type of bait used (fish) may not have been conducive to attracting this benthic feeder. A second possibility is that the species is no longer as abundant as it once was in coastal waters of Northwest Florida, Alabama, and Mississippi. F. Crooke, a commercial shark fisherman who regularly fishes the waters off Orange Beach, Alabama has also noted a marked decline in the number of these sharks taken in the last few years.

TABLE 10

Weight-length relationship for six *Sphyrna mokarran*.

TL(cm)	Wt.(kg)
176	16.3
188	23.1
222	39.9
261	89.4
272	108.0
318	153.8

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SUBSTRATE PREFERENCES OF JUVENILE PENAEID SHRIMPS IN ESTUARINE HABITATS[1]

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ABSTRACT

Various substrates within a tidal creek were characterized, and three common types were selected to test the effects of shrimp size, population density, salinity and temperature on choice of substrate by juvenile brown (*Penaeus aztecus*), white (*P. setiferus*), and pink (*P. duorarum*) shrimp. Substrates selected were sandy-mud (50 to 80% silt-clay, 3.8% organic content), sand (0% organics), and shell (≧ 35% shell and fragments, 3.2% organics). Overall, sandy-mud was selected most frequently by brown (73 to 156 mm TL) and white (87 to 168 mm TL) shrimp. Brown shrimp exhibited affinity for sandy-mud with increased size and increased salinities (21 to 30 $^{0}/_{00}$). Smallest brown shrimp (2.3 to 8.9 g) exhibited decreased preference for sandy-mud at warmest test temperatures (27 to 30 C). Brown shrimp formed aggregations in 52% of the tests, with densities ranging from 3.8 to 6.4 m^{-2}, though average aggregation biomass rarely exceeded 70 g m^{-2}. White shrimp exhibited increased affinity for sandy-mud at cool temperatures (23 C) and high salinities (26 to 29 $^{0}/_{00}$), and formed aggregations of 3.8 to 6.4 shrimp m^{-2} in 50% of the tests. White shrimp size did not significantly influence substrate selection. Pink shrimp (64 to 112 mm TL) exhibited no substrate preference and formed no aggregations when tested at a density of 1.3 m^{-2}; however, 62% of the pink shrimp selected shell when tested in the presence of brown shrimp at a density of 5.1 m^{-2}. Seasonal distributions of juvenile penaeid shrimp in estuarine habitats were hypothesized and supported by field data collected by other investigators. Predicting distributions of benthic organisms through sediment mapping techniques may aid in formulating habitat management policies.

INTRODUCTION

Commercial fishermen along the southeastern and Gulf coast of the U.S. have long recognized the association of adult penaeid shrimp species with specific bottom types and have utilized this knowledge to increase their offshore catches. Adult brown shrimp (*Penaeus aztecus*) prefer mud and silt bottoms in waters 18 to 128 m deep (Hildebrand 1954, 1955; Springer and Bullis 1954; Osborne *et al.* 1969; Nomura and Filho 1970) but are also found on terrigenous muds with sand, mud lumps, or coral rock debris (Kristjonnson 1970). Adult pink

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shrimp (*P. duorarum*) are associated with sand, shell, coral gravel, calcareous mud, and silt-clay bottoms in waters 24 to 46 m deep (Springer and Bullis 1954, Kristjonnson 1970, Brusher and Ogren 1976) but are also abundant in turtle grass (*Thalassia testudinum*) beds (Eldred 1962). Adult white shrimp (*P. setiferus*) prefer mud and silt bottoms less than 35 m deep offshore (Anderson *et al.* 1949; Springer and Bullis 1954; Hildebrand 1954, 1955; Osborne *et al.* 1969; Kristjonnson 1970; Klima 1974).

While the adults remain offshore, postlarval shrimp migrate to nursery areas within estuaries which provide the appropriate combinations of temperature, salinity, substrate, food, and shelter for growth (Broad 1965, Kutkuhn 1966). In North Carolina, shrimp utilize *Spartina* marshes as nursery areas for the first few weeks after arrival in the estuary (Hodson 1979, Weinstein 1979) and then gradually move into tidal creeks and deeper areas of the estuary as they grow (Birkhead *et al.* 1979, Laney 1981). Penaeid shrimp depend upon the substrate for food and shelter (Darnell 1958, Eldred *et al.* 1961, Williams 1965, Dall 1968, Odum and Heald 1972, Giles and Zamora 1973), but only a few studies have been concerned with characterizing the various substrates present within estuaries and their relationship to seasonal distributions of juvenile penaeid shrimp (Mock 1966, Ruello 1973, Weinstein 1979, Geaghan 1980).

Several laboratory studies have examined substrate preferences of penaeid shrimp, but the only factors considered in substrate selection were sediment grain size and food content. Williams (1958) determined that pink shrimp preferred shell-sand, and brown and white shrimp preferred the softer, muddier substrates by introducing them into rectangular troughs containing flowing water and five partially-divided compartments of tidal creek substrates. The week-long tests were conducted with no controlled light level at densities of 14.3 shrimp m^{-2} (20 per test). A randomized latin-square design was utilized to reduce bias caused by the linear arrangement of substrates and the restriction of shrimp movement to only one adjoining compartment at either end of the trough. Shrimp size, animal density, salinity and temperature were noted but not addressed as potential factors influencing substrate selection. Sediment particle size was more important than food content in substrate selection by juvenile school prawns, *Metapenaeus macleayi*, introduced into circular tanks containing still water and four washed substrate types (Ruello 1973). Test length ranged from 8 to 10 hours in covered tanks at densities of 31.4 to 39.3 shrimp m^{-2} (40 to 50 shrimp per test). Similar to Williams (1958) study, salinity, temperature, shrimp size, and animal density were not considered as possible factors affecting substrate choice.

Several laboratory experiments and field studies were conducted to test the following hypotheses: 1) substrate selection by juvenile penaeid shrimp is not based solely on sediment particle size or organic content but is influenced by other factors such as shrimp size, population density, salinity and temperature; and 2) shrimp distribution in tidal creeks during emigration activity can be hypothesized based on substrate types present in the area. Locations of greatest shrimp abundance within the creek-marsh complex were hypothesized and sup-

ported by results of concurrent field investigations. These hypotheses suggest that the loading capacity—biomass (g) per unit area—of a particular substrate within a tidal creek may be determined by shrimp behavior as well as substrate composition. Determining hypothetical distributions of shrimp in estuaries by mapping estuarine sediments may aid in formulating policies regarding habitat management—bulkheading, dredge and fill projects, and placement of coastal water intakes and outfalls.

METHODS

Study Area

The Cape Fear River estuary is located in the southeastern portion of North Carolina, approximately at latitude 33° N and longitude 78° W (Fig. 1). The estuary is narrow and elongated, about 1.6 to 3.6 km in width and 45 km in length from the salt boundary at Wilmington (north) to the river mouth at Baldhead (Smith) Island (south). It is relatively shallow (0.6 to 1.8 m) with the exception of the 12-m deep ship channel dredged and maintained by the U.S. Army Corps of Engineers. Numerous spoil islands, marshes and tidal flats occur throughout the estuary. Tidal creeks cover an estimated 648 ha, and shallow openwater areas between the ship channel and salt marshes contribute an additional 7285 ha (Weinstein 1979). Marsh vegetation in the lower estuary is dominated by smooth cordgrass (*Spartina alterniflora*) and black needlerush (*Juncus roemerianus*). Tidal velocities are high, averaging 1.5 m s^{-1} at the river mouth during ebb tide.

Of the numerous tidal creeks present within the lower Cape Fear River estuary, Walden Creek was chosen for sediment mapping because of its importance as a nursery area for penaeid shrimps (Hodson 1979, Weinstein 1979, Laney 1981) and its proximity to the water intake canal of the Brunswick Steam Electric Plant (BSEP). Walden Creek is formed by the juncture of two tributaries, Nancys and Governors Creeks, and comprises approximately 2.5% of the total marsh acreage in the estuary (Laney 1981). The major portion of the creek is shallow (1 to 3 m) with some deeper portions present upstream (1 to 7 m). Total exchange of waters between the ship channel and Walden Creek occurs in a period of one to two days. Exchange rates in the upper reaches (Nancys and Governors Creeks) range from three to five days, with more rapid exchange occurring during periods of spring tides (Carpenter and Yonts 1979).

The BSEP intake canal was constructed as a 94-m wide cut intersecting Walden Creek near its mouth and bisecting Snows Marsh to join with the ship channel in the Cape Fear River. Average depth in the canal is 5.5 m mean sea level but ranges from 3.5 m at the point of maximum sediment deposition near Walden Creek to 9.8 m near the water intake structure. The cooling system was designed to withdraw 68 m^3s^{-1} of water from the estuary for condenser cooling (Carolina Power and Light Company 1980), which represents approximately five percent of the average exchange rate between the seaward reach of the estuary and the Atlantic Ocean (Carpenter and Yonts 1979). Water flow within the intake canal is unidirectional from the intersection with Walden Creek to the intake structure when the power plant is in normal operation (six of eight circulating water pumps running).

Field Substrate Analyses

The substrates of the BSEP intake canal and portions of the Walden Creek-Snows Marsh system were sampled to determine the composition of local sediments so that representative sediment types could be selected for use in the substrate preference study. On August 15, 1978 substrate samples were collected at each of 46 stations with a Ponar grab sampler. Each sample represented an area of approximately 0.05 m^2 and a maximum depth of about 10 cm in softer sediments. The top 5 cm of sediment was retained and dried at air temperature. Larger oyster shells present in several of the samples were removed and the remaining portion of the

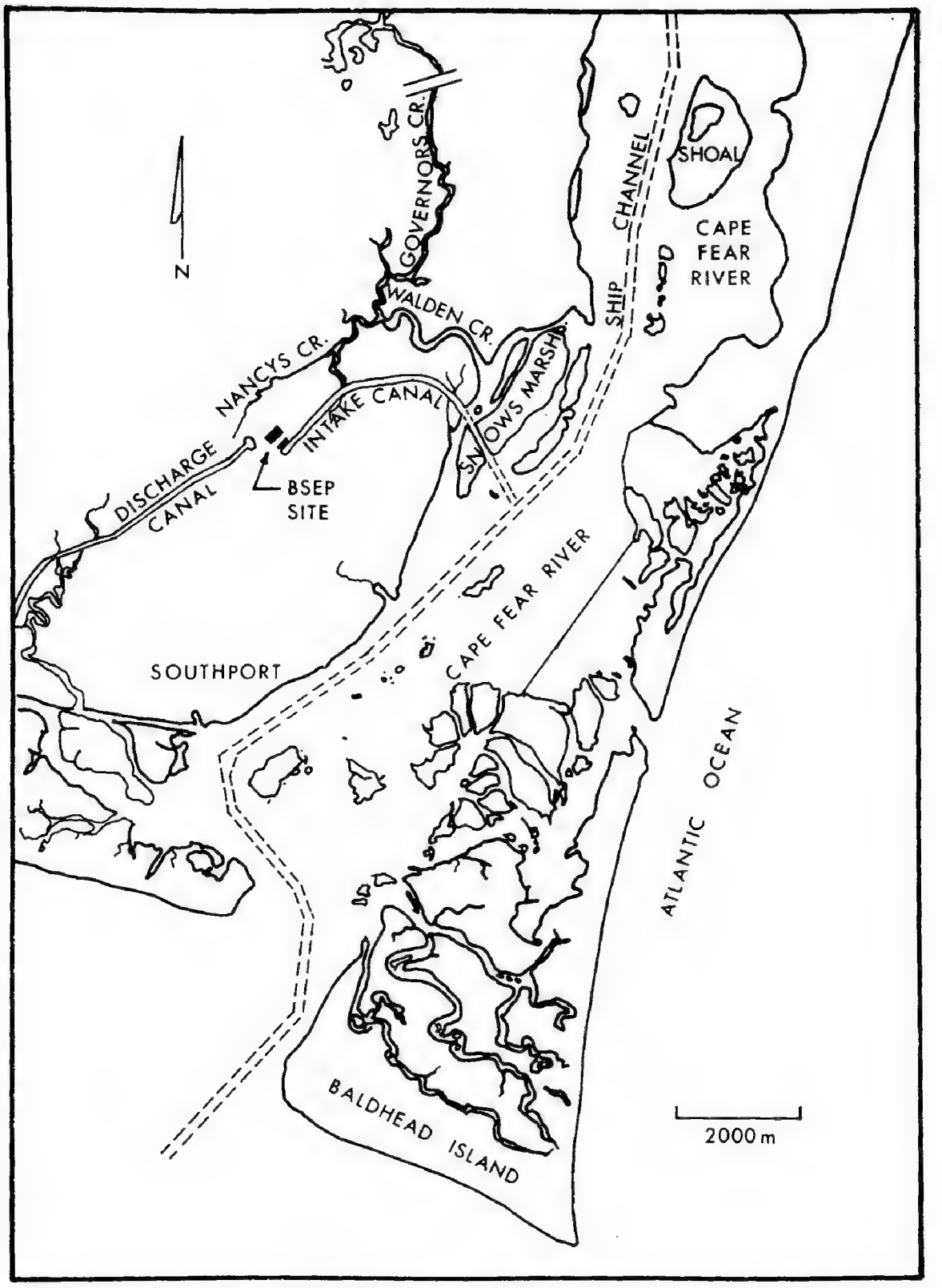

FIG. 1. Cape Fear River estuary showing the lower Walden Creek-Snows Marsh study site and the intake and discharge canals of the Brunswick Steam Electric Plant (BSEP).

sample was dry-sieved through a mesh size of 4.0 mm (−2 ϕ)* to remove smaller shells and debris. Both the shell fraction and remaining sediment fraction (<4.0 mm) were weighed to determine percent shell composition of the whole sample. The sediment portion of the sample was moistened and a commercially available water softener added to facilitate removal of the silt-clay fraction (<0.062 mm, 4 ϕ). The sample was then wet-sieved through mesh sizes of 2.0 mm (−1.0 ϕ), 1.0 mm (0.0 ϕ), 0.5 mm (1.0 ϕ), 0.25 mm (2.0 ϕ), 0.125 mm (3.0 ϕ), and 0.062 mm (4.0 ϕ). Each of these fractions was dried and weighed to determine its percent contribution to the total sample. The organic content of the sediment from each sample site was

* $\phi = -\log_2$ (diameter mm)

determined by the North Carolina Department of Agriculture Soil Testing Laboratory with a modification of the chromic acid oxidation technique (Walkley and Black 1934).

Sediment samples were also collected in December, 1977 in Walden Creek and the BSEP intake canal to detect seasonal changes in organic content and particle size. These samples were analyzed by methods previously described.

Substrate Preference Study

Shrimp were tested for preferred substrates in four circular fiberglass tanks 2.4 m in diameter. The bottom of each tank was divided by wood partitions into six wedge-shaped compartments, each approximately 0.78 m^2 and 10 cm deep. Tanks A, B, and C contained three substrate types—sand, sandy-mud, and shell—which were commonly found within the Walden Creek-Snows Marsh system. Tank D contained only sand and was used as a control. The substrates were placed alternately in the compartments such that each set of opposing compartments contained the same substrate type. The tanks were located outdoors in an area protected by an overhanging roof. This covered area allowed light to enter on the southeast-northwest side of the overhang. A pilot study with wedge partitions in place but no substrate present indicated that wedges closest to the roof edge were avoided by shrimp. To alleviate this problem, the substrate positions of Tank B were rotated one wedge from the positions of Tank A, and the substrate positions of Tank C were rotated two positions from those of Tank A (i.e., Tank A wedge 1 = sandy-mud, B1 = sand, and C1 = shell). The tanks were completely covered with heavy black plastic during testing to prevent light from entering at dawn. Each tank was filled to a depth of 40 cm above the substrate with brackish water from the intake canal during late afternoon just prior to testing. Ambient water temperatures and salinities ranged from 18.0 to 30.9 C and 11 to 30 $^0/_{00}$ during the study.

From July through October, 1978, juvenile penaeid shrimp (64 to 168 mm total length) were collected by trawl from the lower Cape Fear River estuary and held in floating cages located in the canal. Shrimp were removed from the cages, sorted by species, and transferred to the laboratory on each test day approximately two hours before sunset. Six shrimp were used per tank (a density of 1.3 shrimp m^{-2}) to avoid bias in substrate preference due to overcrowding. One of the three substrate types was randomly chosen as the site for introducing the shrimp to the tank. Near dusk, all six shrimp were simultaneously introduced onto the chosen substrate, the covers were positioned over each tank, and the shrimp were left undisturbed until two hours after dawn the following day. At the end of a test, the divider screens which supported the covers during the night were lowered into position and prevented shrimp movement to adjacent wedges. The covers were removed and the water was drained to facilitate locating burrowed shrimp. Total length (TL—tip of rostrum to tip of telson) and weight (g) of each shrimp were recorded in addition to its location of recapture.

Each continuous variable measured throughout the study (temperature, salinity, length and weight) was divided into three classes—low, medium and high values—to permit the use of chi-square analysis. Classes were created based on natural breaks in the distribution over the range of values so that approximately equal numbers of observations fell into each class.

RESULTS

Substrate Profiles

Five substrate types were present within the Snows Marsh, lower Walden Creek, and BSEP intake canal areas (Fig. 2). Four of these types were classified by the proportion of sand (–2.0 ϕ to 4.0 ϕ) and silt-clay (> 4.0 ϕ) particles present in the sample. These were designated as sand (≥90% sand), muddy-sand (50–89% sand), sandy-mud (20–49% sand) and mud (>80% silt-clay). The fifth substrate type was designated as shell (≥35% shell and shell frag-

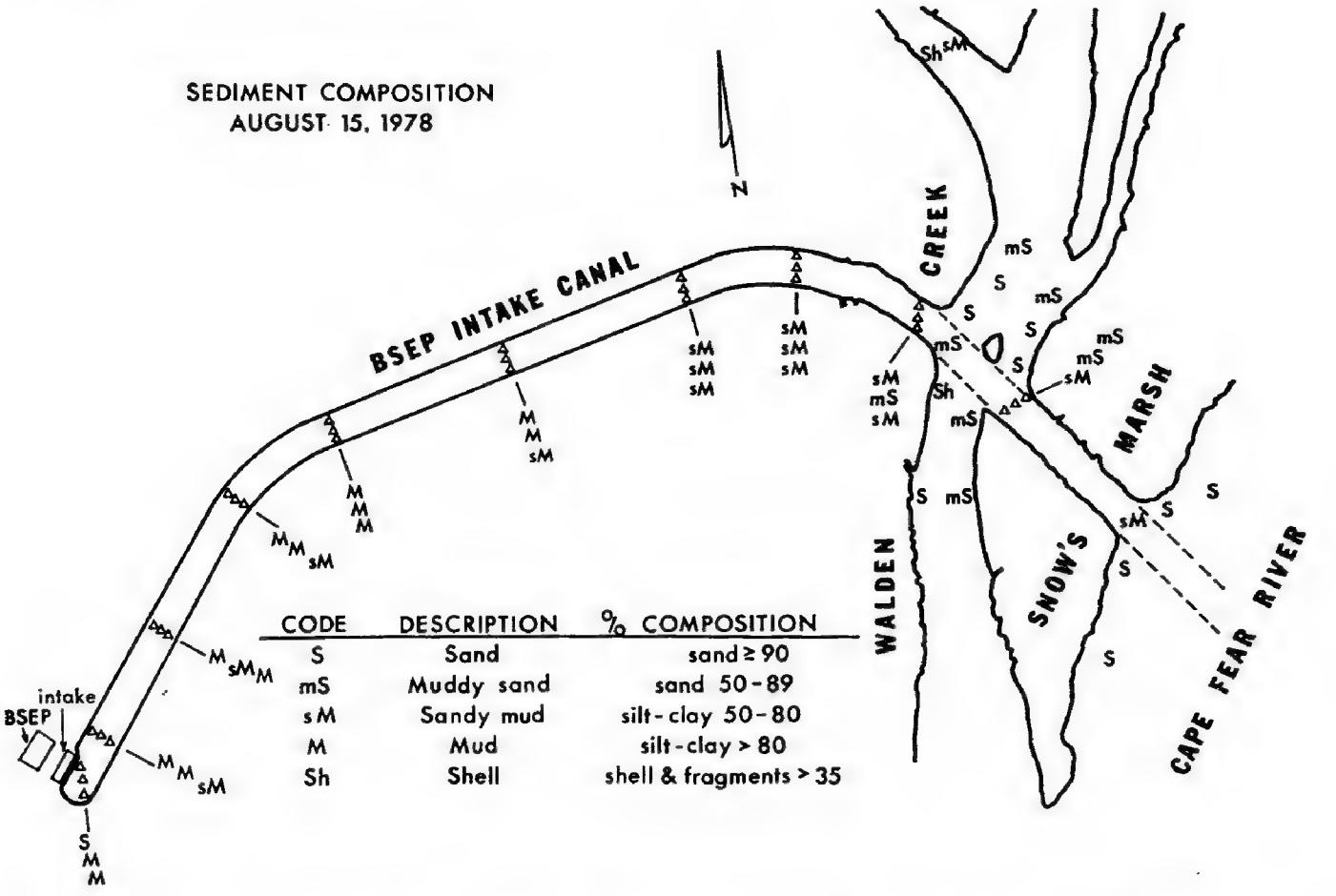

FIG. 2. Textural descriptions of the substrates collected on August 15, 1978 from lower Walden Creek, Snows Marsh, Cape Fear River shallows and BSEP intake canal.

ments) and was composed of large oyster shell mixed with shell fragments, sands and silt-clay particles. Sand occurred most frequently in the shallows of the Cape Fear River between Snows Marsh and the ship channel, and in Walden Creek upstream from its intersection with the canal. Muddy-sand was also common to Walden Creek. Shell was present in two large areas within lower Walden Creek, in the adjacent area downstream from the canal, and also upstream in the first major bend of the creek. Sediments of the intake canal nearest Walden Creek were Sandy-mud, while most sediments of the inner canal (high ground to the intake structure) were composed of mud.

The preponderant particle size of each substrate is an overall reflection of the water velocity most frequently experienced at a particular location. Fine sand (3.0 ϕ) was preponderant in the Walden Creek-Snows Marsh area and the Cape Fear River shallows adjacent to Snows Marsh. Water velocities of 20 to 35 cm s^{-1} are common to these areas (Williams 1978) but can range up to 50 cm s^{-1} (Pendleton and Copeland 1979). Silt-clay particles (>4.0 ϕ) were preponderant in the inner canal which is indicative of weak currents near the bottom.

The amount of organic matter present in the sediments was correlated with its location in the marsh-creek system (Fig. 3). Organic content was highest in the intake canal, ranging from 1% at the scoured, deep area directly in front of the intake structure to 5.2% in the straight midsection. Organic content was lower in the Walden Creek-Snows Marsh area and the Cape Fear River shal-

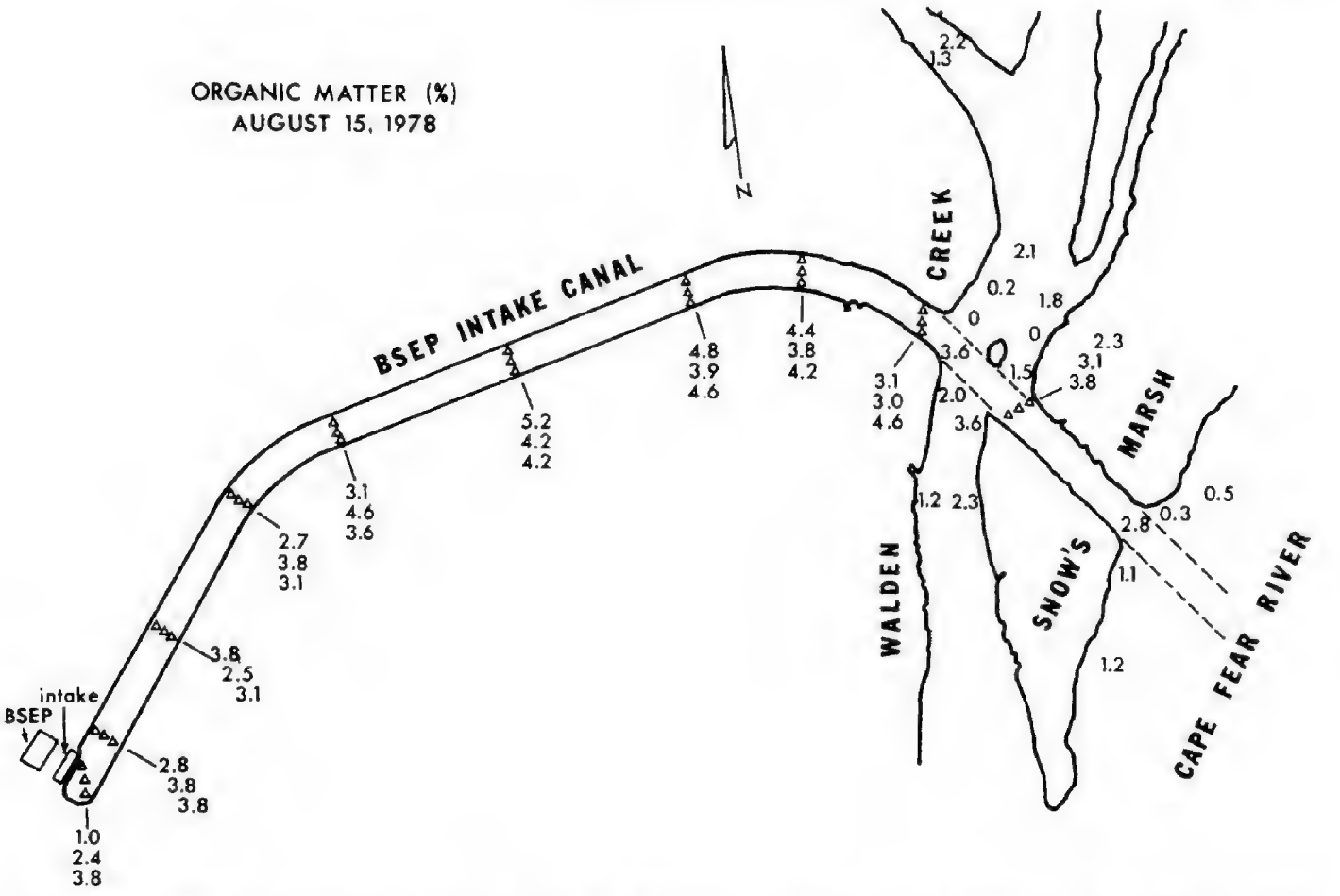

FIG. 3. Percent organic matter of the substrates collected on August 15, 1978 from lower Walden Creek, Snows Marsh, Cape Fear River shallows and BSEP intake canal.

lows, ranging from 0.0 to 3.8%. There was no seasonal fluctuation of organic content or particle density (g cc^{-1}) in Walden Creek and canal sediments ($P > .05$) using Wilcoxon signed rank test of significance for matched pairs (two-tailed).

P. aztecus

Of all tests containing only brown shrimp, 52% resulted in three or more shrimp burrowed in the same wedge (Table 1). This represented densities ranging from 3.8 to 6.4 shrimp m^{-2} (3 to 5 shrimp per wedge). The majority of these aggregations occurred on sandy-mud. Even though the number of brown shrimp in an aggregation fluctuated with each test, the average biomass in the aggregation rarely exceeded 70 g m^{-2} (Table 1).

Sandy-mud (20–49% sand) was the substrate selected most frequently by brown shrimp regardless of the substrate type upon which they were placed to begin the experiment. There apparently was no differential preference between sand and shell except in Tank C. Brown shrimp placed on sand in Tank C were found burrowed in spaces among the shell-dominated substrate the following morning, and brown shrimp placed on shell were later found burrowed in sand ($P < .01$, Chi-square). This pattern was not observed for Tanks A and B and was not significant when data from all tanks were combined for chi-square analysis.

Although sandy-mud was the preferred substrate for juvenile brown shrimp, substrate selection was influenced by shrimp size, salinity and temperature.

TABLE 1

Juvenile brown shrimp, *P. aztecus*, which formed aggregations of three or more shrimp in the same wedge (from a total of 84 tests involving only brown shrimp).

Shrimp in one wedge	Number per sq. meter	Total number of occurrences	Substrate	No. of Occur-rences	Mean Density (gm^{-2})	Range (gm^{-2})
3	3.8	29 (35%)	Sandy-mud	18	46.3	27.8-81.4
			Shell	3	36.8	31.2-41.2
			Sand	4	31.0	13.2-47.8
			Tank D	4	40.0	28.6-49.0
4	5.1	9 (11%)	Sandy-mud	5	68.9	51.0-110.8
			Shell	2	72.7	54.6-90.8
			Sand	0		
			Tank D	2	56.9	46.3-67.6
5	6.4	5 (6%)	Sandy-mud	4	67.4	61.3-76.8
			Shell	0		
			Sand	0		
			Tank D	1	60.4	

Larger brown shrimp chose sandy-mud more frequently (P = .04) than smaller shrimp (Table 2). All shrimp size classes selected sandy-mud with greater frequency (P = .01) at highest salinities while preference for sand decreased (Table 3). For smallest brown shrimp tested (2.3 to 8.9 g), there was a decreased preference (P = .04) for sandy-mud at warmer temperatures (Table 3).

P. duorarum

Pink shrimp ranging in size from 64 to 112 mm TL (2.2 to 11.1 g) were tested during late summer and fall at temperatures 18.0 to 28.9 C and salinities 10 to 30 ‰. Chi-square analysis of the data indicated no substrate preference

TABLE 2

Effects of length and salinity on choice of substrate by juvenile brown shrimp, *Penaeus aztecus*, analyzed by chi-square tests. sM = sandy-mud, S = sand, Sh = shell.

Variable	N	X^2	df	P	Class	Range	Preferred Substrate (%) N	sM	S	Sh
Total Length (TL)	377	10.194	4	0.04	TLCL 1	73-104 mm	128	45.3	27.3	27.3
					TLCL 2	105-114	119	55.5	20.2	24.4
					TLCL 3	115-156	130	64.8	18.5	25.6
Starting Salinity	316	17.227	4	0.01	SSCL 1	11.0-16.9‰	102	42.7	34.6	22.7
					SSCL 2	17.0-20.9	138	48.1	27.2	24.7
					SSCL 3	21.0-30.0	76	58.8	18.7	22.5

TABLE 3

Two-factor effects of variables weight (WTCL) and starting temperature (TSCL) on choice of substrate by juvenile brown shrimp, *Penaeus aztecus*, analyzed by chi-square tests. sM = sandy-mud, S = sand, Sh = shell.

Variable	Range	N	X^2	df	P	Controlling Variable	Range	Preferred Substrate (%) N	sM	S	Sh
WTCL 1	2.3-8.9g	135	9.9	4	0.04	TSCL 1	20.6-27.4 C	33	63.3	12.1	24.3
						TSCL 2	27.5-28.6	51	43.1	27.3	19.6
						TSCL 3	28.7-30.3	51	41.2	23.5	35.3

for pink shrimp, and none of the continuous variables tested as classes (weight, length, temperature or salinity) were found to be significantly associated with substrate selection (Rulifson 1980). This result may have been due to an insufficient number of observations for pink shrimp (N = 76). Extraordinarily cold winters during 1976–77 and 1977–78 reduced pink and white shrimp populations within the Cape Fear River estuary (Schwartz *et al.* 1979) which made it difficult to obtain sufficient numbers for testing. No more than three pink shrimp were found burrowed in the same wedge (3.8 m^{-2}) throughout the study.

P. setiferus

Of the 20 tests involving only white shrimp, 50% resulted in three or more shrimp burrowed in the same wedge (Table 4). The majority of these aggregations occurred on sandy-mud. No white shrimp aggregations were observed in Control Tank D.

TABLE 4

Juvenile white shrimp, *P. setiferus*, which formed aggregations of three or more shrimp in the same wedge (from a total of 20 tests involving only white shrimp).

Shrimp in one Wedge	#m^{-2}	Total Number of Occurrences	Substrate	Number of Occurrences	Mean Density (g m^{-2})	Range (g m^{-2})
3	3.8	7 (35%)	Sandy-mud	5	65.51	53.59-74.36
			Shell	1	74.74	
			Sand	1	57.95	
			Tank D	0		
4	5.1	2 (10%)	Sandy-mud	1	100.39	
			Shell	1	91.03	
			Sand	0		
			Tank D	0		
5	6.4	1 (5%)	Sandy-mud	0		
			Shell	0		
			Sand	1	136.28	
			Tank D	0		

Substrate selection by white shrimp was influenced by temperature and salinity. Increasing temperatures decreased white shrimp affinity for sandy-mud (50.0 to 25.8%) while increasing affinity for shell (8.3 to 35.5%) (Table 5). Increased salinity resulted in increased choice of sandy-mud (27.0 to 50.8%) and decreased affinity for shell and sand (Table 5). Size of white shrimp and the substrate type upon which they were placed to begin the experiment did not significantly influence ($P > .05$) substrate selection.

Density

Results of the study presented above demonstrated that brown and white shrimp formed aggregations of three or more in the same wedge in a large number of tests, and the highest density aggregations occurred almost exclusively on sandy-mud. Furthermore, the aggregations appeared to be limited by the amount of biomass within the wedge, as the aggregations never included all six shrimp in the experiment.

To test this hypothesis, the stocking density of shrimp in the tanks was changed so that Tank B contained a species mixture of 48 individuals (10.3 m^{-2}) and Tanks A, C, and D contained 24 individuals (5.1 m^{-2}). Since all wedges in Control Tank D were similar with respect to sand grain size and organic content (0.0%), it was expected that the brown, pink and white shrimp would disperse rather uniformly throughout the tank with respect to biomass. In the other three tanks, uniform distribution was expected only if the loading capacities of all three substrate types were exceeded due to the stocking density. Under these conditions, salinity and temperature effects on substrate selection were expected to be minimal.

At the conclusion of the tests, no large aggregations were observed in Control Tank D. The 24 shrimp which had been introduced onto one wedge to start the test had dispersed themselves rather uniformly throughout five of the six sand wedges at densities no greater than 90 g m^{-2} (Table 6). There was an indication that distribution throughout the tank was clumped according to species.

Results from Tank C indicated shrimp were dispersed throughout the tank according to the loading capacities of the substrates. In the previous tests, pink

TABLE 5

Effects of starting temperature (TSCL) and starting salinity (SSCL) on choice of substrate by juvenile white shrimp, *P. setiferus*, analyzed by chi-square tests. sM = sandy-mud, S = sand, Sh = shell.

Variable	N	X^2	df	P	Class	Range	Preferred Substrate (%) N	sM	S	Sh
Starting Temperature	102	9.827	4	0.04	TSCL 1	23.0-23.4 C	24	50.0	41.7	8.3
					TSCL 2	23.5-25.1	47	48.9	21.3	29.8
					TSCL 3	25.2-28.3	31	25.8	38.7	35.5
Starting Salinity	102	6.249	2	0.05	SSCL 1	20-25 ‰	37	27.0	35.1	37.8
					SSCL 2	26-29	65	50.8	29.2	20.0

TABLE 6

Dispersal of shrimp introduced on one wedge in Control Tank D during the density study.

		Number Introduced	Wedges 1 through 6					
			Sand	Sand	Sand	Sand*	Sand	Sand
Species	Brown	7	1	0	1	3	2	0
	White	9	3	2	1	2	1	0
	Pink	8	1	1	1	0	4	1
Density	$\#m^{-2}$	5.1	6.4	3.8	3.8	6.4	9.0	1.3
	gm^{-2}	57.6	89.2	36.4	47.2	86.7	81.0	5.0
Average shrimp size (g)			13.9	9.6	12.4	13.5	9.0	5.0

* Wedge of introduction.

shrimp exhibited no substrate preference; however, when tested in the presence of brown shrimp, 68% of the pink shrimp selected shell, and 42% of those were found burrowed in the same wedge. This formed the largest aggregation in the tank (10.3 pink shrimp m^{-2}), but due to their small size (average of 4.56 g) only represented a density of 46.92 g m^{-2}. Their size enabled them to utilize the small sandy-mud niches between the shells as shelter. Pink shrimp of similar size were also found burrowed in sand (21%) and sandy-mud (11%). Brown shrimp were larger than pink shrimp, averaged 10.0 to 12.52 g, and selected sandy-mud (80%) and sand (20%). Greatest shrimp density in Tank C occurred on sandy-mud but did not exceed 61 g m^{-2} (Table 7).

In Tank A, a large aggregation of white shrimp comprising 63% of the

TABLE 7

Dispersal of shrimp introduced on one wedge of Tanks, A, B and C during the density study.

		Tank	Number Introduced	Sandy-mud	Sand	Shell	Sandy-mud	Sand	Shell
Species	White	A	24**	1	2	6	9	2	3
Density	$\#m^{-2}$		5.1	1.3	2.6	7.7	11.5	2.6	3.8
	gm^{-2}		88.7	25.7	40.0	139.2	232.3	41.0	54.2
Average shrimp size (g)				19.8	15.4	18.1	20.2	15.8	14.3
Species	Brown	B	22**	1	1	2	12	3	2
	White		24	9	6	1	4	1	3
	Pink		2	0	0	0	0	0	2
Density	$\#m^{-2}$		10.3	12.8	9.0	3.8	20.6	5.1	9.0
	gm^{-2}		185.1	221.3	153.3	68.2	455.5	89.6	122.8
Average shrimp size (g)				17.2	17.0	17.5	22.1	17.6	13.7
Species	Brown	C	5	1	1	0	3	0	0
	Pink		19	0	0	8	2	4	5
Density	$\#m^{-2}$		5.1	1.3	1.3	10.3	6.4	5.1	6.4
	gm^{-2}		31.0	16.2	13.3	46.9	60.9	21.3	27.6
Average shrimp size (g)				12.4	10.3	4.6	9.5	4.2	4.3

* Wedge of introduction.

** One not accounted for after termination of test.

number introduced were found burrowed in adjacent wedges of sandy-mud and shell. The largest single aggregation occurred on the sandy-mud wedge of introduction (38%) at a density of 232.31 g m^{-2} (11.5 white shrimp m^{-2}). The adjacent wedge with shell substrate contained the remaining 25% of the aggregation at a density of 139.23 g m^{-2} (7.7 white shrimp m^{-2}). The larger white shrimp selected sandy-mud ($P < .05$), while smaller shrimp chose sand and shell (Table 7).

Tank B contained 22 brown and 24 white shrimp which dispersed according to species and formed two large aggregations on opposite sides of the tank. Each aggregation was centered on a wedge which contained sandy-mud. The majority (55%) of the brown shrimp were found burrowed in the wedge of introduction with an additional 23% located on the sand and shell wedges to either side of the introduction site. The majority (75%) of the white shrimp were found burrowed in wedges on the opposite side of the tank. A large proportion (38%) were burrowed in sandy-mud with a density of 221.28 g m^{-2}, a value similar to that of the white shrimp aggregation formed in Tank A (232.31 g m^{-2}). The remainder of the white shrimp aggregation (38%) was located on the adjacent sand and shell wedges. Only 17% of the white shrimp remained on the wedge of introduction with brown shrimp, resulting in a density of 455.51 g m^{-2} (20.6 shrimp m^{-2}). The two pink shrimp introduced into Tank B were found burrowed together in shell substrate (Table 7).

DISCUSSION

The distribution of juvenile penaeid shrimp in estuarine habitats can be explained from the results of this study. In general, juvenile brown shrimp will be found in greatest abundance in estuarine areas with sandy-mud or mud bottoms. Smaller brown shrimp (< 100 mm TL) in lower salinity (< 17 ‰), upstream areas and in shallow, high temperature areas (> 28 C) will occur in only slightly greater concentrations on sandy-mud bottoms. As juvenile brown shrimp grow and emigrate slowly through tidal creeks and the lower estuary toward the ocean (salinity increasing), their preference for sandy-mud bottom will greatly increase and ultimately determine their offshore distribution as adults. Juvenile white shrimp exhibit greatest estuarine abundance during summer, the period when nursery areas are normally experiencing moderate salinities and warm temperatures. Relative abundance of juvenile white shrimp will be slightly greater on sand and shell-dominated bottoms and slightly less on sandy-mud. As temperatures decrease during fall and white shrimp slowly emigrate to lower estuarine areas, their affinity for sandy-mud bottoms will increase significantly and influence offshore distributions as adults. Juvenile pink shrimp will be found on all three bottom types in similar concentrations, a characteristic which will prevail through adulthood. Because brown shrimp appear to be the dominant species, estuarine distribution of pink and white shrimp may be shifted to less preferred habitats for a portion of the summer when all three species are present.

Field data collected by seine (Weinstein 1979) and trawl (Schwartz *et al.* 1979, Geaghan 1980, Laney 1981) suggest that distribution patterns of juvenile penaeid shrimp in Walden Creek and adjacent areas were similar to distributions predicted from laboratory results. Greatest average annual abundance of juvenile brown shrimp occurred on mud, sandy-mud, and muddy-sand bottoms (Table 8) in Walden Creek downstream from its intersection with the BSEP intake canal, and in the canal from the straight mid-section to the intake structure on the BSEP plant site (Fig. 2). Similar distribution was observed for juvenile white shrimp, while juvenile pink shrimp abundance was consistently low in all areas. During May, 1977, sand bottoms in Walden Creek headwaters (Nancys Creek) contained peak concentrations of postlarval and juvenile brown shrimp (18 to 64 mm TL), estimated at 1.31 m^{-2}, which occurred at low salinities (8.6 ‰ ± 6.8 SD) and moderate temperatures (21.4 C ± 8.1 SD) (Wein-

TABLE 8

Distribution of brown, pink and white shrimp (shrimp m^{-2}) in the Cape Fear River, lower Walden Creek, and BSEP intake canal determined from trawl data presented in Schwartz *et al.* (1979) and collected during studies by Geaghan (1980) and Laney (1981). Values are averages for the indicated sampling period and were adjusted by assuming trawls were 30% efficient and sampled 60% of the headrope length.

Area		Brown No.per sq.meter	Pink No.per sq.meter	White No.per sq.meter	Total No.per sq.meter	Source
Cape Fear River, East shoal (sand)	Jan 1978 to Dec 1978				<.01	Schwartz (1979)
Cape Fear River, West shoal (sand)	May 1977 to Nov 1978	<.01	.01	<.01	.01	Geaghan (1980)
	Jan 1978 to Dec 1978				<.01	Schwartz (1979)
Canal,intersecting Walden Creek, and through Snows Marsh (sandy-mud)	May 1977 to Dec 1978	.01	.02	<.01	.03	Geaghan (1980)
	Jan 1978 to Dec 1978				.03 to .05	Schwartz (1979)
Walden Creek upstream from canal (sand)	Jan 1974 to Jul 1976	<.01	<.01	<.01	.01	Laney (1981)
Walden Creek downstream from canal (muddy-sand)	May 1977 to Nov 1978	.02	.01	<.01	.03	Geaghan (1980)
	Jan 1974 to Jul 1976	.02	<.01	.03	.06	Laney (1981)
West edge of Walden Creek to high ground (sandy-mud)	Jan 1978 to Dec 1978				<.01	Schwartz (1979)
Mid-canal (mud)	May 1977 to Nov 1978	.06	.02	<.01	.08	Geaghan (1980)
	Jan 1978 to Dec 1978				.01	Schwartz (1979)
Inner canal near power plant (mud)	May 1977 to Nov 1978	.06	.02	.01	.09	Geaghan (1980)
	Jan 1978 to Dec 1978				.02	Schwartz (1979)

stein 1979). Lower Walden Creek sediments did not contain peak shrimp concentrations until July, 1975 (Laney 1981). Three species present on sandy-mud bottom downstream from the canal-creek intersection comprised a density of 1.37 m^{-2}. Brown shrimp were present in greatest biomass (2.08 g m^{-2}) but were not numerically dominant (0.39 m^{-2}). White shrimp were dominant in numbers (0.89 m^{-2}) but not in biomass (0.94 g m^{-2}). Pink shrimp were present in low numbers (0.10 m^{-2}) and biomass (0.05 g m^{-2}). Shrimp abundance on the adjacent sand bottom upstream from the canal-creek intersection was much lower, and only two species were collected. Brown shrimp (0.06 m^{-2}, 0.46 g m^{-2}) and white shrimp (0.07 m^{-2}, 0.59 g m^{-2}) were collected in nearly equal numbers and biomass. Adequate field data were not available to test statistically effects of salinity and temperature on substrate selection.

Apparently the substrate preferences of sub-adults exhibited during final emigration activity are retained as adults residing offshore. In this study, juvenile brown shrimp exhibited increased affinity for sandy-mud as the season progressed; adults offshore are found in greatest abundance on mud and silt bottoms (Hildebrand 1954, 1955; Springer and Bullis 1954; Osborne *et al.* 1969; Nomura and Filho 1970). Juvenile white shrimp also exhibited a seasonally increased preference for sandy-mud; adults offshore prefer mud and silt bottoms (Anderson *et al.* 1949; Springer and Bullis 1954; Hildebrand 1954, 1955; Osborne *et al.* 1969; Klima 1974). In this study, juvenile pink shrimp indicated no substrate preference; adults offshore are found on all bottom types—sand, shell, and silt-clay bottoms (Springer and Bullis 1954, Kristjonnson 1970, Brusher and Ogren 1976).

Although substrate selection by juvenile penaeid shrimp appears to be a seasonally changing process, the day-to-day selection must involve food availability. Penaeid shrimp are omnivores and feed on detritus, plant material, polychaetes, bacteria, algae, and other microfauna present on the substrate surface (Darnell 1958, Eldred *et al.* 1961, Williams 1965, Odum and Heald 1972, Dall 1968). Although substrates in marshes and headwaters of tidal creeks contain large amounts of organic matter (Mock 1966, Weinstein 1979), estuarine muds contain less than 10% organic material and only a portion of it is directly usable as a food source for animals (Dall 1968). Juvenile brown and white shrimp in the present study selected the substrate which contained the highest percentage of organic material available (sandy-mud, 3.8%). However, the shell-dominated substrate was similar to sandy-mud in organic content (3.2%) but was not chosen by larger brown shrimp, which indicated that other factors were used as criteria for substrate selection.

Substrates must also be selected on the basis of composition as compared to shrimp size. Sediment grain size, not food content, affected the distribution of juvenile school prawn, *Metapenaeus macleayi*, in laboratory tests (Ruello 1973). Adult pink shrimp were observed to burrow in hard substrates of sand and sand-shell and entered soft bottoms within a few seconds (Fuss and Ogren 1966). Burrow depth of pink shrimp and substrate composition were not correlated, but pink shrimp size (body depth) was correlated with degree of pene-

tration into the sediment (Fuss 1964). Williams (1958) noted smallest brown shrimp were often found on shell-sand among the interstices at the surface, whereas large individuals were usually found in softer bottoms. Results of the present study indicated that largest brown shrimp preferred sandy-mud and avoided shell-dominated substrate. In addition, the majority of brown and white shrimp aggregations occurred on sandy-mud even when stocking densities were 10.3 shrimp m^{-2}. These results suggest that burrowing locations in shell-dominated bottoms are restricted in number, and the exact number available is determined by shell size and density in addition to size of the shrimp. Available burrowing sites (*i.e.*, loading capacity of the substrate) should therefore be controlled by the concentration of biomass within an area which shrimp can physically and behaviorally tolerate.

Competition for habitat among the three shrimp species may occur during certain periods of the year. For several weeks during summer, white and pink shrimp populations are in the presence of brown shrimp populations in Cape Fear River habitats (Birkhead *et al.* 1979, Hodson 1979, Weinstein 1979, Laney 1981). In the laboratory, brown and white shrimp tested together formed species aggregations at opposite sides of the tank on their preferred substratum (sandy-mud). Species segregation may indicate the dominance of one species over another. The fact that brown shrimp were found on the wedge of introduction and white shrimp were located on the opposite side of the tank suggests that brown shrimp are dominant over white shrimp and will displace them in nature. A similar conclusion was reached by Giles and Zamora (1973), who reported that both brown and white shrimp preferred grass beds when tested separately; when placed together, brown shrimp remained in the grass beds and the majority of white shrimp were found on barren substrate.

Penaeid shrimp emigrating from high marsh areas and tidal rivulets during ebb tide must rely on environmental cues for appropriate timing of events. One of these cues may involve water movement in combination with decreasing water depth. In this study, emergence activity by the majority of burrowed shrimp (over 90% were burrowed at test termination) was elicited by draining the tank at the completion of a test. Shrimp emerged from the substrate and moved in the direction of water flow (toward the center of the tank) until divider screens were contacted or water depth became too shallow and thus caused difficulty in movement. They then burrowed back into the sediment unless prevented by their location (i.e., clumps of shell).

Understanding the behavior of penaeid shrimps and other benthic organisms and realizing how these behavioral patterns are affected by physical and chemical alterations to their immediate environment are important considerations when formulating habitat management policies. The increased burden placed upon nursery areas through multiple use—e.g., bulkheading, channelization, dredge and fill projects, and placement of water intakes and outfalls—necessitates restricting development to areas which are not extensively used for the growth and production of the many commercially-important fish and shellfish stocks nurtured in estuarine habitats. Habitat management in the Cape Fear

Estuary is no exception. The construction of the BSEP water intake canal through a primary nursery area created a new estuarine habitat characterized by deep, slow-moving water. The altered water flow patterns within lower Walden Creek and deposition of silt-clay muds in the canal created prime shrimp habitat. Because Walden Creek is such a productive area for populations of juvenile penaeid shrimp, the optimal qualities of the canal probably serve to increase their susceptibility to impingement on the screens of the water intake structure. A prior understanding of habitat utilization and the behavioral patterns of juvenile organisms within the local area could have been used to design or site the canal in a location better suited for minimizing damage to these populations. Since these aspects were not considered, the power company has spent millions of additional dollars on mitigative measures such as water flow reduction and the installation of diversion screens at the Walden Creek-canal intersection.

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THE OCCURRENCE OF HYPOXIC BOTTOM WATER OFF THE UPPER TEXAS COAST AND ITS EFFECTS ON THE BENTHIC BIOTA

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ABSTRACT

Hypoxic bottom water occurred off the upper Texas coast in May–July 1979 after heavy spring runoff and a diatom bloom. Benthic assemblages at two study sites off Freeport, Texas decreased from spring densities of 3000–4000 individuals/m^2 to 300–600 individuals/m^2 by late July. Species diversity also decreased and perturbations occurred in the Shannon-Weiner diversity indices. Of the dominant taxa, polychaetes were least affected by hypoxia and amphipods and echinoderms the most affected. Storm-caused waves in late July initiated the breakup of hypoxic conditions; these conditions had completely abated by late September. A short-lived irruption occurred immediately afterward as depopulated bottoms were reinvaded. Diversity and abundances appeared to be returning to more normal conditions by early 1980.

INTRODUCTION

Mass mortality of marine benthic communities due to hypoxia (< 2.0 ppm of dissolved oxygen) has been a widely reported phenomenon. Much of the available literature was reviewed by Brongersma-Sanders (1957) who discussed many factors contributing to low dissolved oxygen (D.O.) levels. Two factors pertinent to the present study were water column stratification and calm weather periods. Both factors inhibit vertical mixing and cause oxygen depletion in bottom waters, especially during summer when chemical and biological oxygen demands are greatest. The importance of the oxygen-hydrogen sulfide interaction was emphasized because the interface between the two gases rises above the sediment as oxygen is depleted.

In the Gulf of Mexico, large scale hypoxia (i.e. excluding dredged canals and small embayments) has been reported in Alabama and Louisiana. In Mobile

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Bay, Alabama, periodic mass migrations of demersal fish and crustaceans into shallow water during summer occur in response to shoreward movement of hypoxic deeper waters (Loesch 1960, May 1973). This phenomenon, known locally as a "jubilee", is promoted by several factors, such as decomposition of organic matter, salinity stratification and decreased vertical mixing during calm weather.

The occurrence of hypoxic bottom waters off the Louisiana coast west of the Mississippi Delta is apparently a recurrent, if not annual, phenomenon. The Mississippi and Atchafalaya Rivers discharge large volumes of fresh water laden with organic material during spring. Salinity stratification and reduced vertical mixing permit the D.O. content of bottom water to decrease below 2.0 ppm. Benthic macroinvertebrates suffer mortalities and nektonic species leave the area. The extent of the hypoxic area varies; it apparently depends on the amount of fresh water discharged. During a multi-year (1973–76) investigation of central Louisiana continental shelf waters, hypoxia was first detected in May 1973 between the 6 and 37-m isobaths. The layer was 2 to 7 m thick and in some instances the recorded D.O. was 0.0 ppm. The areal extent was largest in July and smallest in December. Between 1974 and 1976 the area became smaller, concomitant with reduced freshwater discharge (Flowers, Miller and Gann 1975; Harris, Ragan and Kilgen 1976; Harris, Ragan and Green 1978; Ragan, Harris and Green 1978). Oxygen reduction off Louisiana in 1973–74 was also noted by Farrell (1974) who simultaneously found reduced numbers of benthic individuals. In 1978 hypoxia caused an extensive mortality of benthos off the Louisiana coast south of Morgan City. Trawl samples collected between 6 and 17-m depths contained many dead or moribund epifaunal organisms: sea catfish (*Arius felis*) were the only fish collected. Divers also reported many dead invertebrates on the bottom (Fotheringham and Weissberg 1979).

The present study is the first documented offshore occurrence of hypoxia along the Texas coast, and is one of few in which two different communities of benthic invertebrates were sampled regularly before, during and following a hypoxic event, which allowed study of the effects on, and rate of recovery of, the affected benthic assemblages.

STUDY AREA

Macrobenthic samples were collected approximately monthly at two sites offshore from Freeport, Texas (Fig. 1). Both sites were sampled as part of a baseline environmental study conducted for the Department of Energy prior to offshore disposal of nearly saturated brine. Brine is produced by leaching salt from Bryan Mound salt dome near Freeport to create oil storage caverns as part of the Strategic Oil Reserve program. The nearshore site [originally designated as the brine disposal location, but abandoned because of potential disruption of white shrimp (*Penaeus setiferus*) spawning activities] was 8 km offshore in 15 to 17-m depth. The offshore site was 19 km offshore in 21-m depth. Fifteen stations were sampled at each site, with identical station arrangements at both sites. The station pattern was designed to detect the effects of discharged brine on the bethic communities, and has no bearing on this report. Although the project is still in progress, data analysis for this report will be concerned only

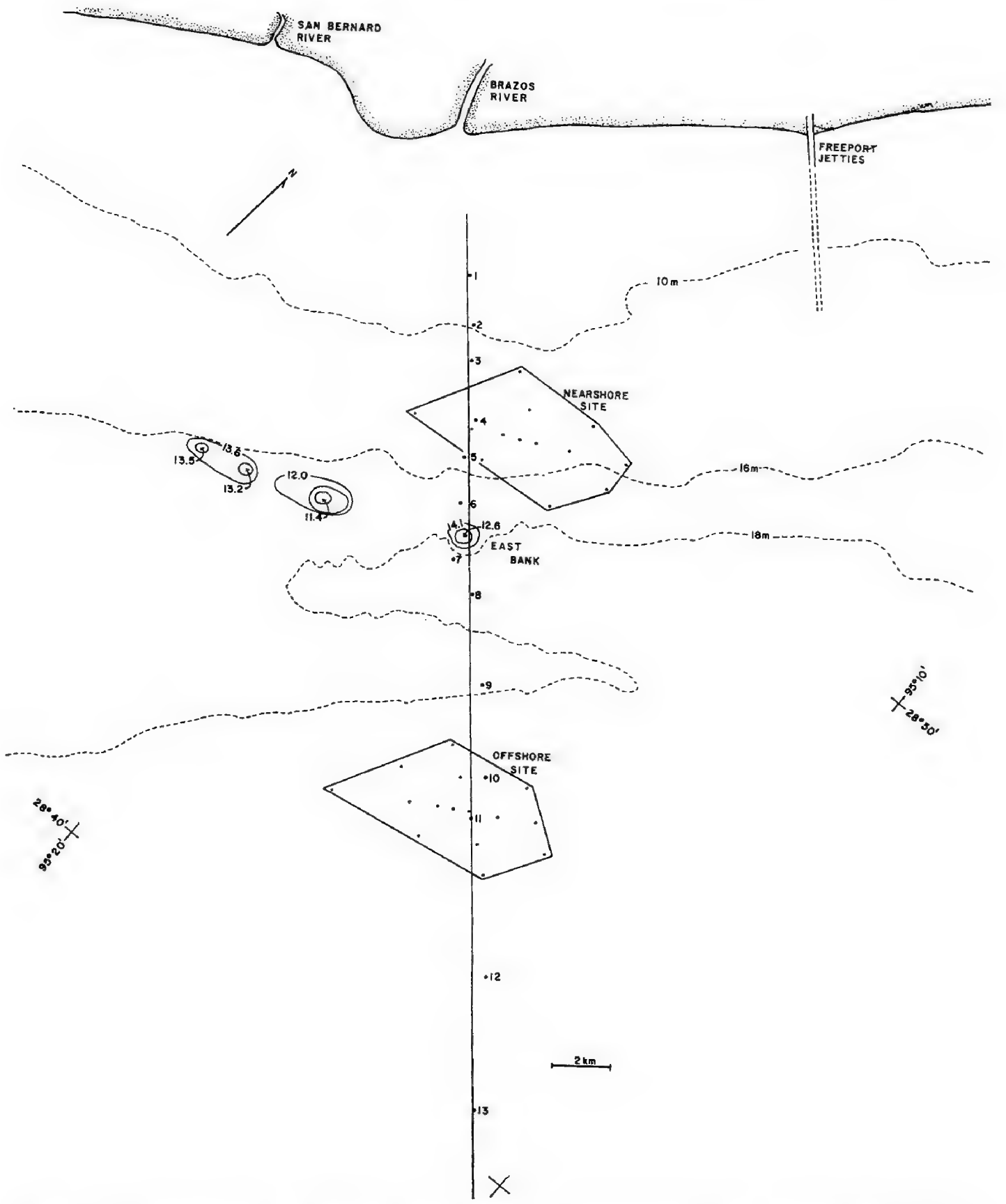


FIG. 1. Chart of the area offshore from Freeport, Texas showing the locations of the nearshore and offshore study areas, East Bank, and the cross shelf transect sampled on 8 July 1979.

with the pre-brine disposal phase of the study, i.e. 28 collections at the nearshore site (September 1977 to March 1980) and 27 collections at the offshore site (December 1977 to March 1980).

FIELD TECHNIQUES

The macrobenthos were sampled in triplicate by SCUBA divers. Three Ekman grabs (232 cm^2 each) attached to a line having an anchor at one end and a buoy at the other, were

lowered overboard when the vessel came on station. Divers descended the line from the buoy. The Ekman grabs were moved to an undisturbed location, pushed into the bottom by hand, triggered, and the vent flaps were secured with elastic bands. While on the bottom the divers collected a water sample, and if the water was clear visually examined the bottom for large organisms, burrows and animal tracks. Since January 1979 sediment samples have been collected at the offshore site with either a fourth Ekman grab or in diver-carried plastic jars. Our sampling method was quite successful. The vessel did not have to be anchored, and a station occupation in 21-m depth was only 7 to 10 minutes. All stations in a study area were sampled in 4 hours or less, which eliminated variability of populations due to multi-day sampling.

When the Ekman grabs were brought aboard the vessel, the contents were placed in plastic tubs where the sediment temperature was measured and a sediment description, based on visual and textural examination, was recorded. Samples were then washed on a 0.5 mm mesh sieve and the material retained on the sieve was fixed in 5% seawater-formalin. Sediment samples were placed in jars.

The temperature and salinity of surface and bottom water samples were recorded from the beginning of the study. D.O. measurements began in October 1978. Prior to January 1979, temperature was measured with a Celsius thermometer, salinity with a refractometer and D.O. with a Hach kit; since then temperature and salinity have been determined with a YSI Model 33 T-S-C meter, and D.O. with a YSI Model 57 dissolved oxygen meter.

LABORATORY TECHNIQUES

The day after collection, benthic samples were washed with fresh water on a 0.5 mm mesh sieve, then preserved in rose bengal-stained 70% ethanol. Each sample was subsequently examined microscopically and all organisms were removed, identified to lowest possible taxon, and counted. Sediment samples were dried and then analyzed for grain size using the methods of Folk (1974), which included sieve sorting of sand fractions and pipette analysis of silts and clays.

DATA ANALYSIS

The data were analyzed descriptively by comparing numbers of species and individuals at each study area and by relating changes in these numbers to trends in the abiotic data. The data were also subjected to cluster analysis, principal components analysis and analysis of variance (ANOVA). ANOVA of mean log transformed total abundance and mean Shannon-Weiner index of diversity was determined and the hierarchy of means was tested for significance using Duncan's multiple range test.

Cluster analysis used the Bray-Curtis dissimilarity index, flexible sorting, and both log and cube root transformation (Clifford and Stephenson 1975). Those species occurring 10 or more times, comprising about 95% of all individuals, were used in the analyses. Principal components analysis used the 25 most abundant species.

RESULTS

Abiotic Characteristics of the Study Areas

Sediments

The nearshore site was located on the Recent subaqueous delta of the Brazos River. Sediments were primarily consolidated, layered or mottled, red and gray silts and clays that were covered with a thin (0.5–2 cm) veneer of soft silt-clay during relatively calm weather periods.

The offshore site was located on the drowned Pleistocene delta of the Brazos-Colorado River (Neinaber 1958, 1963). Sediments were principally sand to

sand-silt-clay; mean grain sizes were in the 5ϕ to 7ϕ range, although considerable variability was found at any given station from month to month. As at the nearshore site, a thin silt-clay veneer covered the bottom during calm weather periods.

Temperature

Seasonal sediment temperature fluctuations tended to be similar at both sites. Spring temperature increases were slightly slower at the offshore site, but organisms were subjected to similar temperature regimes (Fig. 2). At both sites the sediment temperature was usually similar to the bottom water temperature, but was up to 5 C cooler than the surface water in early summer (Tables 1, 2). Annual sediment temperature trends were similar; the temperature was lowest in January–February and highest in July–August. The principal differences in annual temperature variations were: 1) in the fall–winter of 1977–78 the temperature cooled more rapidly and remained lower longer than in following years; and 2) the relatively mild winter of 1979–80 in which recorded temperatures did not fall below 13 C, and rose briefly to 16 C during a warming period in January 1980.

Salinity

The nearshore site experienced a much greater variation in the bottom salinity than the offshore site because of closer proximity to freshwater sources (Fig. 2). The nearshore salinity varied between 25 and 35 ppt whereas the deeper offshore water remained within 30–35 ppt during most of the study. There was, however, a pronounced trend toward lower offshore salinities during the study period (Fig. 2). We also noted that the water column tended to be more isohaline during rough sea states than on calm days.

The salinity of the nearshore site, and to a lesser degree, the offshore site, is influenced by both local river discharge and by Mississippi River discharge (Temple, Harrington and Martin 1977). Two pronounced decreases in salinity occurred during the study, February–June 1979, during which time stratification became quite pronounced (Tables 1, 2), and August 1979–January 1980, but which did not appear to produce any adverse effects. Very heavy rainfall during these periods caused flooding along the rivers emptying into upper Texas coastal waters, and sent large quantities of fresh water into the Gulf of Mexico. Surface salinities were at or below 30 ppt during most of 1979 and bottom waters were less than 30 ppt several times at the nearshore site. The offshore bottom water salinity was lower than 30 ppt only once, in September 1979. Thus the organisms at the nearshore site experienced a much less stable salinity regime.

Dissolved Oxygen

The D.O. of bottom waters at both sites tended to be similar in concentration and seasonal variation (Fig. 2). The D.O. was high (8.0 ppm) during the

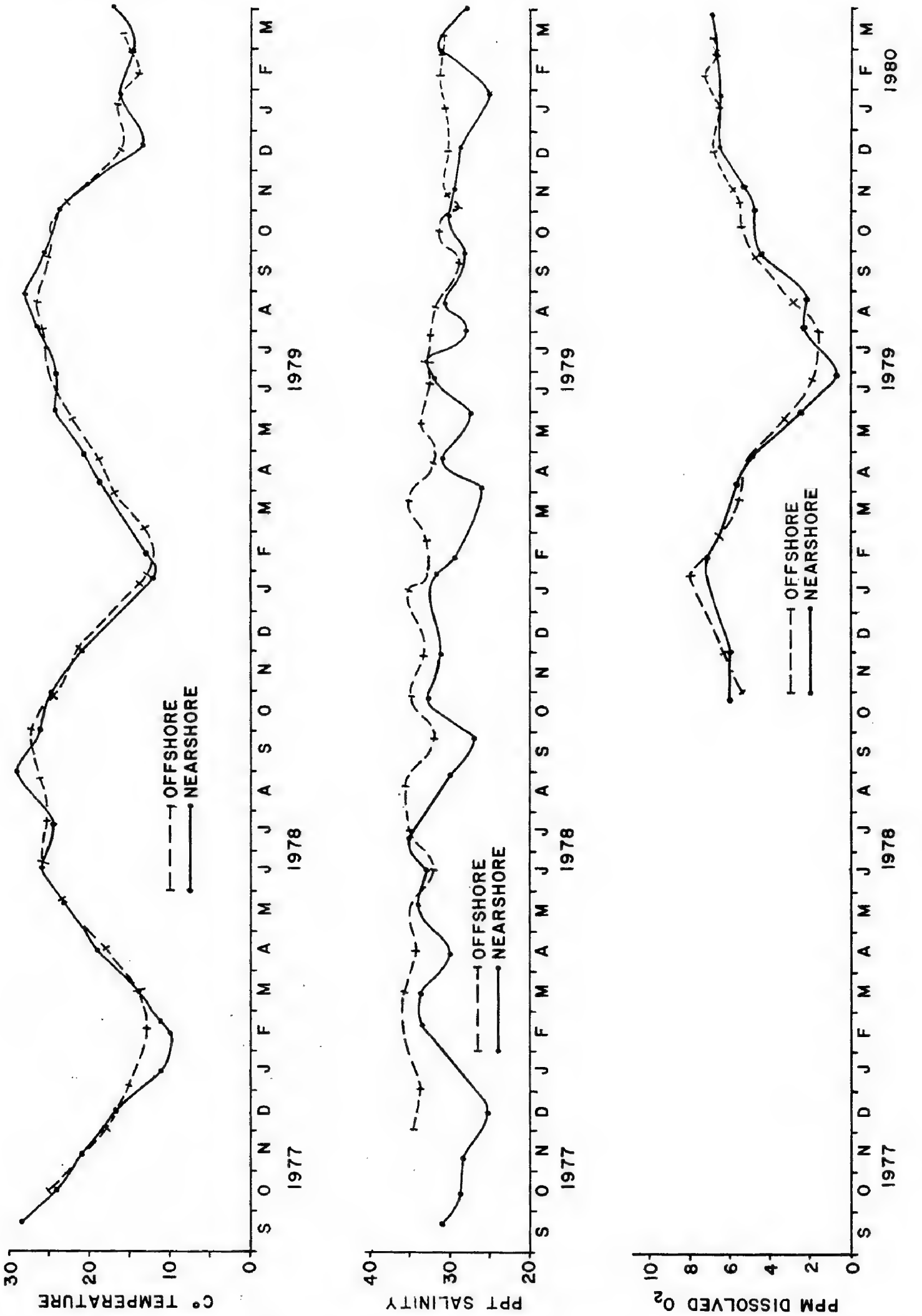


FIG. 2. Comparison of the seasonal trends of sediment temperature, bottom water salinity, and dissolved oxygen at nearshore and offshore study areas.

TABLE 1

Comparison of the average monthly temperature, salinity and dissolved oxygen of the surface and bottom of the water column and the sediment temperature at the nearshore site. △ indicates difference between surface values and either the sediment or bottom water, whichever is appropriate.

	Temperature				Salinity			Dissolved Oxygen		
	Surface	Bottom	Sediment	Δ	Surface	Bottom	Δ	Surface	Bottom	Δ
1977										
22 Sep	29.1	28.7	28.6	0.5	30.3	31.0	0.6			
14 Oct	23.5	23.4	24.0	0.5	28.5	28.6	0.1			
11 Nov	21.3	20.8	21.9	0.5	28.0	28.1	0.1			
15 Dec	16.1	16.8	16.8	0.7	22.8	25.2	2.4			
1978										
14 Feb	8.5	10.0	10.0	1.5	--	--				
20 Feb	10.2	10.8	11.3	1.1	27.8	33.5	5.7			
15 Mar	14.5	14.0	14.0	0.5	31.2	33.7	2.5			
14 Apr	21.3	20.1	18.9	2.4	26.5	30.1	3.6			
26 May	26.8	25.4	23.3	3.3	29.9	33.9	4.0			
16 Jun	29.7	28.2	25.9	3.8	28.0	33.0	5.0			
13 Jul	30.1	24.9	24.5	5.6	33.1	35.2	2.1			
31 Aug	29.4	30.5	29.4	0.0	28.3	29.9	1.6			
28 Sep	28.0	28.0	26.2	1.8	25.1	26.7	1.6			
25 Oct	24.6	24.1	25.0	0.4	31.4	32.3	0.9	---	6.0	---
1 Dec	20.3	21.3	21.2	0.9	25.7	31.2	4.5	---	6.0	---
1979										
28 Jan	12.0	12.0	11.8	0.2	32.0	32.0	0.0	8.2	7.7	0.5
13 Feb	13.9	12.7	12.9	1.0	24.9	29.4	4.4	8.8	7.3	1.5
5 Apr	20.7	21.4	18.7	2.0	23.5	26.2	2.7	6.5	5.7	0.8
26 Apr	23.1	22.0	20.7	2.4	22.7	31.1	8.4	5.5	5.0	0.5
1 Jun	25.6	24.6	24.4	1.2	24.3	27.5	3.2	5.5	2.5	3.0
28 Jun	29.3	25.0	24.3	5.0	19.8	32.0	12.2	5.6	0.7	4.9
8 Jul	28.0	25.0	--	---	27.5	33.0	5.5	4.5	2.0	2.5
2 Aug	28.1	27.5	26.8	1.3	28.0	30.4	2.4	4.9	3.3	1.6
23 Aug	28.0	27.8	28.2	0.2	27.6	30.8	3.2	5.4	3.2	2.2
26 Sep	24.1	25.0	25.6	1.4	22.5	28.4	5.9	6.3	4.5	1.8
29 Oct	22.9	23.1	23.9	1.0	26.7	30.5	3.8	6.5	4.8	1.7
19 Nov	19.1	19.5	20.5	1.4	27.1	29.4	2.4	6.3	5.4	0.9
19 Dec	13.5	14.2	13.7	0.2	26.7	28.5	1.8	7.6	6.9	0.7
1980										
28 Jan	13.2	13.8	16.3	3.1	24.1	25.1	1.0	7.5	6.7	0.8
28 Feb	14.1	13.4	14.5	0.4	29.1	30.9	1.8	7.3	6.9	0.4
31 Mar	17.8	17.6	17.8	0.0	26.1	28.2	2.1	7.4	6.9	0.5

winter when solubility increased and the water was turbulent. D.O. decreased as the water warmed during the spring. Surface waters (Tables 1, 2) remained well oxygenated at all times (> 4.0 ppm) but the bottom water D.O. fell below 2.0 ppm in June and July 1979 at both sites, during and following pronounced water column stratification. This event (hypoxia) had profound biological effects. D.O. concentrations increased above 3.0 ppm once the stratification was disrupted and continued to increase as the water cooled toward the end of the year. D.O. maxima were again recorded during the winter months.

Characteristics of the Benthic Communities

Benthic communities at the two sites were composed of different assemblages of organisms, as might be expected because of different abiotic characteristics

TABLE 2

Comparison of the average monthly temperature, salinity and dissolved oxygen of the surface and bottom of the water column and the sediment temperature at the offshore site. Δ indicates the difference between the surface values and either the sediment or bottom water, whichever is appropriate.

	Temperature				Salinity			Dissolved Oxygen		
	Surface	Bottom	Sediment	Δ	Surface	Bottom	Δ	Surface	Bottom	Δ
1977										
2 Dec	21.2	19.9	17.9	3.3	28.6	34.5	5.9			
1978										
4 Jan	14.0	14.5	15.0	1.0	33.5	33.9	0.4			
24 Feb	10.9	11.8	12.9	2.0	--	--	---			
17 Mar	14.0	14.0	14.0	0.0	32.3	35.7	3.4			
15 Apr	21.2	20.3	17.9	3.3	29.3	34.4	5.1			
24 May	24.7	24.8	23.2	1.5	30.2	34.9	4.7			
20 Jun	28.6	27.7	26.0	2.6	30.0	31.9	1.9			
17 Jul	30.7	27.0	25.4	5.3	33.1	35.1	2.0			
21 Aug	30.1	28.0	26.5	3.6	34.5	35.7	1.2			
27 Sep	27.9	28.6	27.4	0.5	31.5	32.0	0.5			
30 Oct	24.8	25.3	24.3	0.5	33.7	35.0	1.3	---	5.4	---
30 Nov	21.4	22.9	21.6	0.2	31.1	33.6	2.5	---	6.7	---
1979										
17 Jan	14.7	14.4	14.1	0.6	34.6	35.7	1.1	---	---	---
28 Jan	13.0	13.0	13.0	0.0	32.5	32.7	0.2	8.1	8.0	0.1
26 Feb	13.4	13.7	13.5	0.1	28.4	32.6	4.2	7.8	6.6	2.2
25 Mar	18.2	17.2	17.1	1.1	26.4	35.2	8.8	6.0	5.6	0.4
24 Apr	22.8	21.2	19.1	3.7	20.1	32.9	13.2	7.4	5.3	2.1
24 May	24.5	23.0	22.1	2.4	25.3	33.8	8.5	5.7	3.3	2.4
25 Jun	30.3	25.0	25.0	5.3	19.4	32.8	13.4	6.2	1.9	4.3
8 Jul	28.0	24.5	--	---	28.5	33.5	5.0	4.4	1.0	3.4
30 Jul	28.0	26.2	26.2	1.8	28.4	32.5	4.1	5.4	1.6	3.8
21 Aug	28.7	26.9	26.8	1.9	30.5	32.0	1.5	5.2	2.9	2.3
24 Sep	24.5	25.5	25.5	1.0	24.7	28.7	4.0	6.4	4.8	1.6
18 Oct	25.1	24.7	25.0	0.1	30.3	31.6	1.3	5.6	5.5	0.1
15 Nov	19.9	20.5	20.8	0.9	30.3	30.5	0.2	6.1	5.9	0.2
16 Dec	15.2	15.6	16.0	0.8	30.9	32.2	1.3	7.0	6.8	0.2
1980										
18 Jan	15.4	15.2	16.5	1.1	28.8	30.6	1.8	6.9	6.7	0.2
13 Feb	13.7	14.1	14.1	0.4	30.8	31.7	0.9	7.5	7.5	0.0
27 Feb	15.1	14.9	15.0	0.1	29.5	30.9	1.4	7.5	6.4	1.1
10 Mar	16.0	16.0	15.9	0.1	26.7	31.3	4.6	7.6	5.4	2.2

(sediment, depth, salinity). The offshore site had a higher species diversity* (232 vs. 209 species) and larger numbers of individuals (75434 vs. 57267 total individuals) than the nearshore site (Table 3). Polychaetous annelids numerically dominated both assemblages with amphipod crustaceans being the second most abundant. The combined polychaete and amphipod abundances overwhelmingly dominated the offshore assemblage, but were less dominant at the nearshore site. About 90% of all individuals collected at each site belonged to the 20 most abundant species at that site and the polychaete *Paraprionspio pinnata* was the overall numerical dominant at both sites. Only 12 of the 20 species occurred in both lists, and their relative dominance was usually dissimilar (Table 4).

* Diversity is used in its original sense of numbers of species.

TABLE 3

Comparison of the community characteristics of the offshore and nearshore study areas (all data summed).

	Offshore	Nearshore
Total number of species	232	209
Total number of individuals	75434	57267
Percent of species occurring at all 15 stations	20.3	16.3
Percent of species occurring at 10 or more stations	31.9	30.1
Percent of species occurring at 5 or more stations	48.3	51.2
Percent of species occurring at only 1 station	33.6	30.1
Total polychaetes	60701 (80.5%)	35969 (62.8%)
Total amphipods	9558 (12.7%)	3636 (6.7%)
Total bivalves	1908 (2.5%)	9685 (19.9%)
Total nemerteans	1477 (2.0%)	2467 (4.3%)
Total hemichordates	75 (0.1%)	2422 (4.4%)
Total "others"	1715 (2.2%)	2422 (4.4%)

Cluster analysis and ordination results indicated the assemblages at stations within study areas were similar, but the higher degree of similarity occurred at the offshore site, as shown by the dendrogram (Fig. 3) and the concentration of ordination spikes (Fig. 4). The nearshore stations had a lower degree of occurrence of species that separated the 15 stations into two sub-clusters (Figs. 3, 4).

TABLE 4

Comparison of the 20 most abundant species at the offshore and nearshore study areas. Also listed are the total numbers of individuals and the cumulative percentage of the total assemblage.

	Offshore Site			Nearshore Site		
Rank	Species	No. of Individuals	Cumulative Percentage	Species	No.of Individuals	Cumulative Percentage
1.	*Paraprionospio pinnata**	24869	34.0	*Paraprionospio pinnata**	20655	43.0
2.	*Nereis micromma**	6642	43.1	*Abra aequalis*°	5773	55.0
3.	*Ampelisca abdita*+	5425	50.6	*Magelona phyllisae**	3907	63.1
4.	*Aricidea* cf. *taylori**	5322	57.9	*Ampelisca agassizi*+	2511	79.3
5.	*Magelona phyllisae**	3862	63.2	*Cerebratulus lacteus*	1841	72.1
6.	*Lumbrineris verrilli**	3246	67.7	*Mediomastus californiensis**	1232	74.7
7.	*Prionospio cristata**	2692	71.4	*Nereis micromma**	1180	77.2
8.	*Armandia maculata**	1730	73.8	*Armandia maculata**	1018	79.3
9.	*Mediomastus californiensis**	1690	76.1	*Ampharete americana**	813	81.0
10.	*Ampelisca verrilli*+	1688	78.4	*Nephtys incisa**	667	82.4
11.	*Prionospio cirrobranchiata**	1624	80.6	*Sigambra tentaculata**	591	83.6
12.	*Cossura delta**	1282	82.4	*Balanoglossus* sp.	532	84.7
13.	*Photis macromanus*+	1034	83.8	*Diopatra cuprea**	402	85.5
14.	*Ampelisca agassizi*+	1008	85.2	*Photis macromanus*+	396	86.3
15.	*Nephtys incisa**	601	86.0	*Cossura delta**	361	87.1
16.	*Cerebratulus lacteus*	564	86.8	*Ampelisca abdita*+	355	87.8
17.	*Tharyx marioni**	563	87.6	*Lumbrineris verrilli**	340	88.5
18.	*Corbula operculata*°	505	88.3	*Cirratulus hedgpethi**	319	89.2
19.	*Ceratocephale* sp.*	490	89.0	*Polydora ligni**	319	89.8
20.	Nemertean (yellow band)	462	89.6	*Phoronis architecta*	305	90.4
	Others	5789	100.0	Others	4567	100.0

* - Polychaeta
\+ - Amphipoda
° - Bivalvia

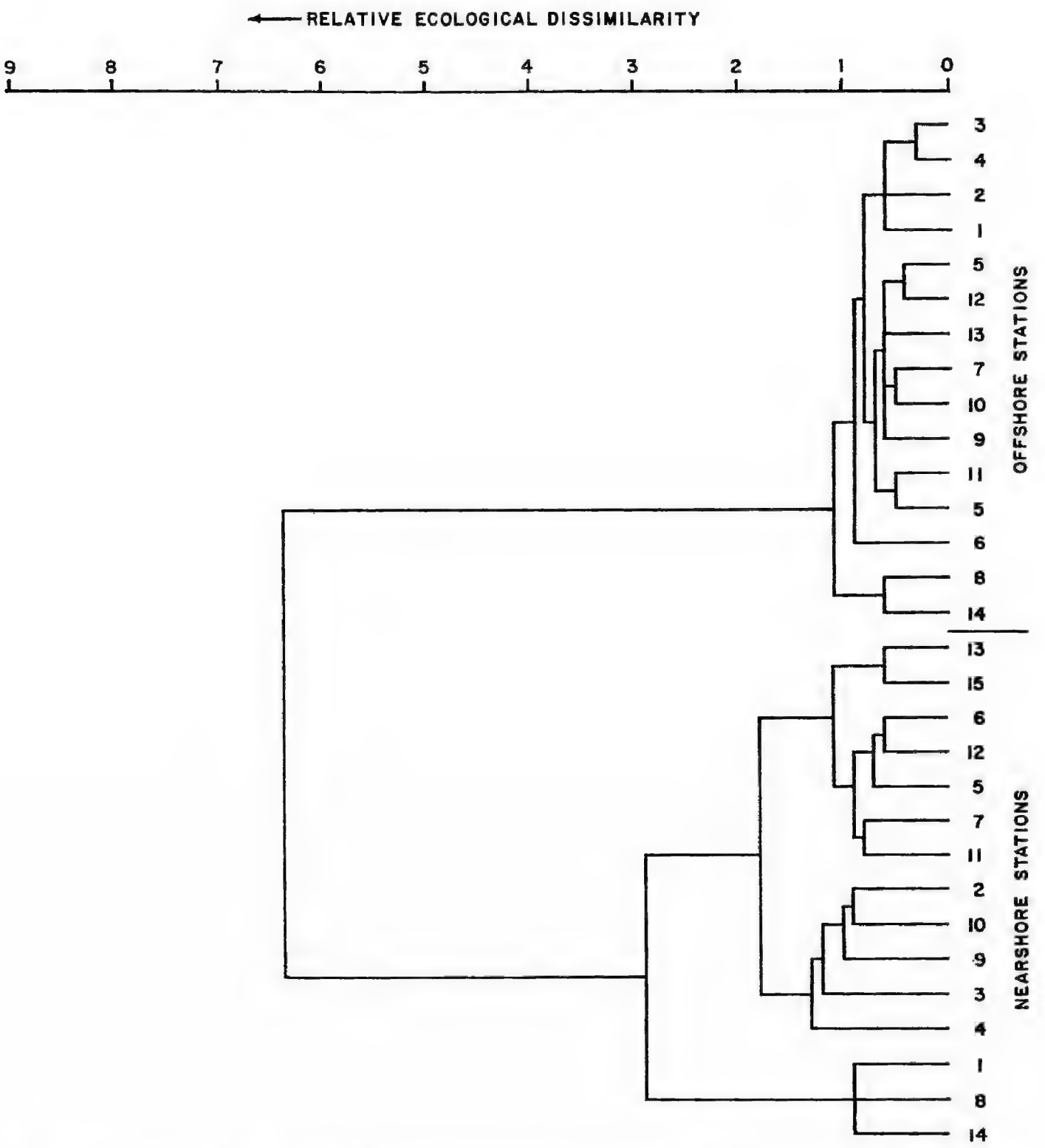
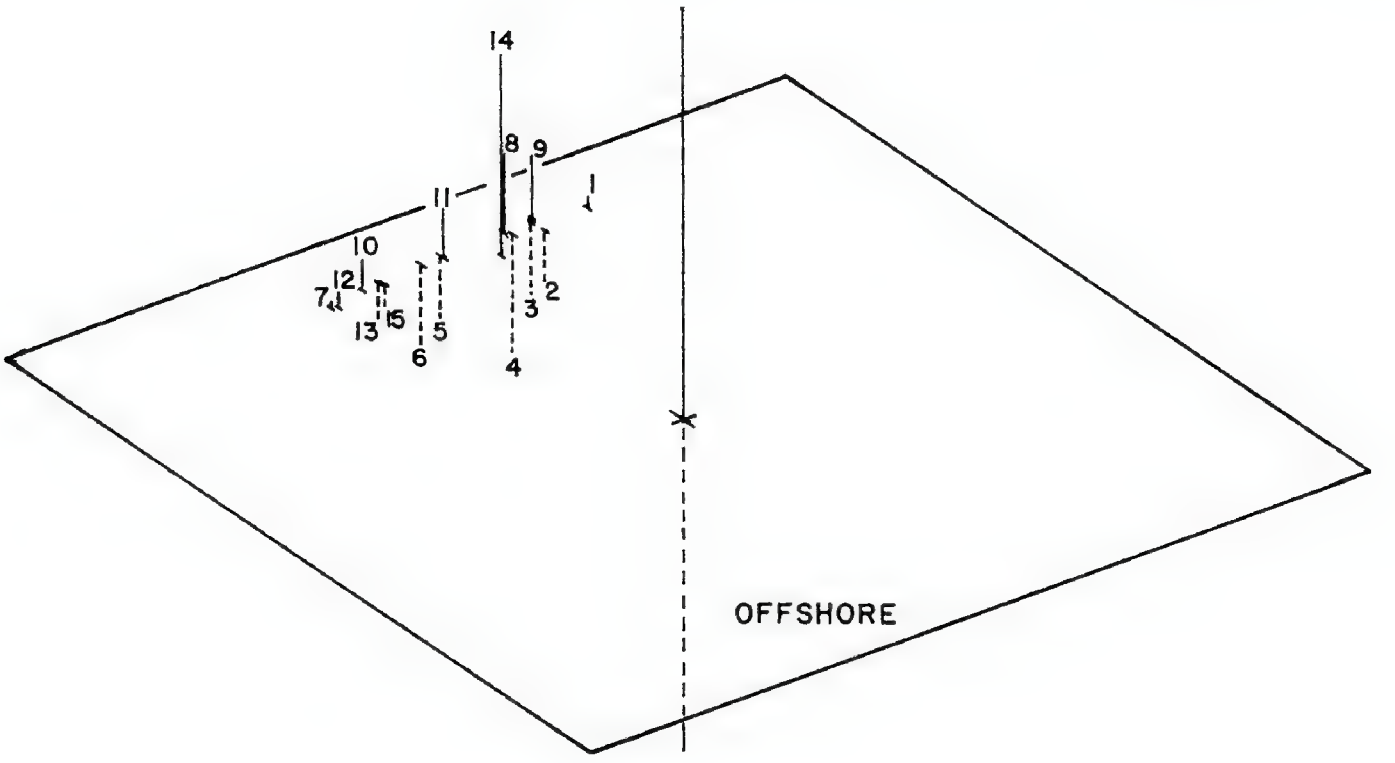


FIG. 3. Dendrogram showing the station groups formed by cluster analysis of combined nearshore and offshore data.

Onset, Extent and Breakup of Hypoxia

Two events occurred which probably contributed to stratification of the water column. First, the spring of 1979 was unusually wet (NOAA 1979a, b) and the rivers discharged large volumes of fresh water. Second, excepting a brief period of strong winds in mid-June, winds were mostly light to moderate and were dead calm during the last week of June.

D.O. decreased from winter maxima of 8.0 ppm to about 2.5–3.0 ppm by late May coincident with increasing temperatures. Bottom water first became minimally hypoxic around the first of June because a few nearshore stations had



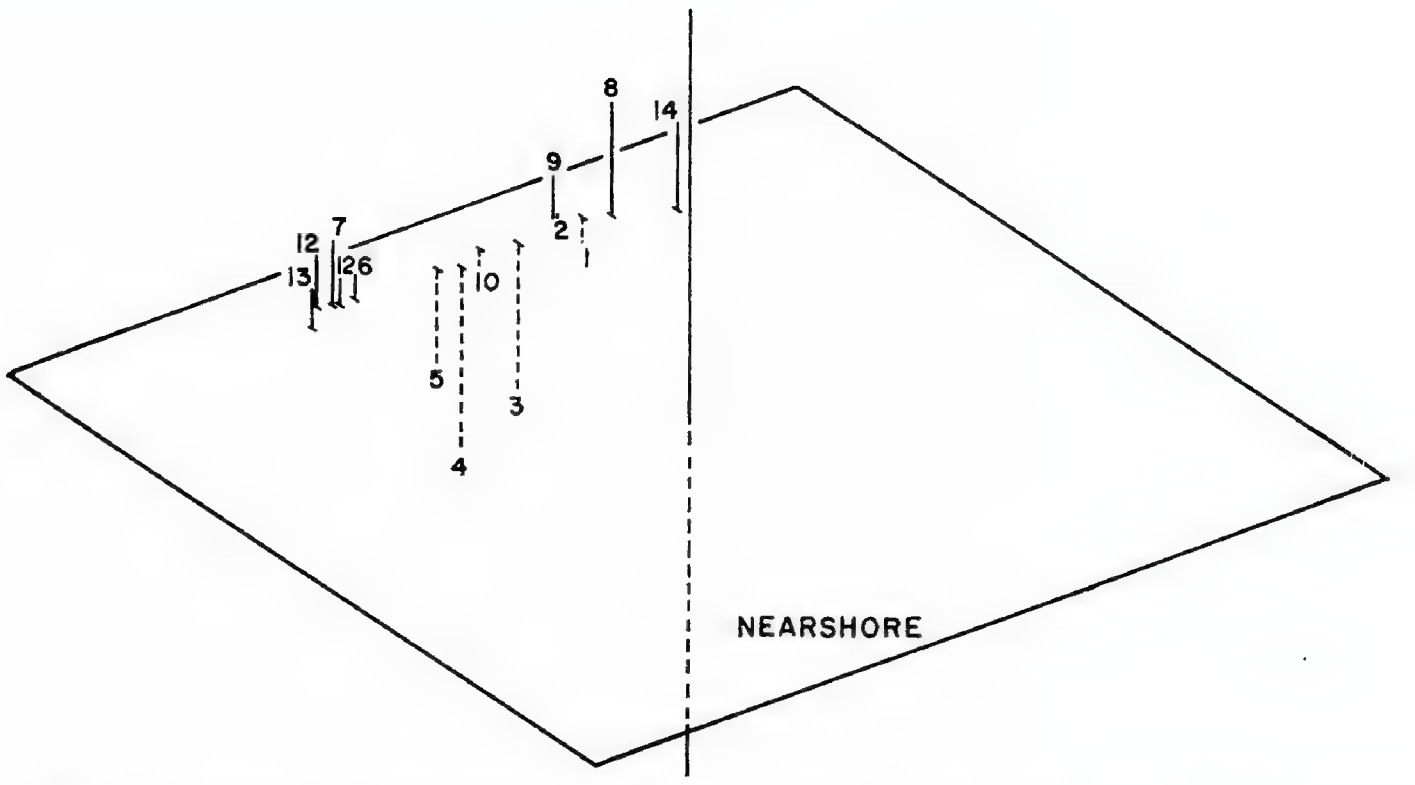


FIG. 4. Comparison of results of principal components analysis of offshore and nearshore data. Dashed lines indicate negative values with respect to the plane.

< 2.0 ppm D.O. on 1 June. Hypoxia apparently first occurred near shore and spread seaward, or was more intense near shore. On 25 June, the offshore site was barely hypoxic (average 1.9 ppm D.O.). Three days later (28 June), the nearshore site bottom water varied from 0.5 to 1.7 ppm, but averaged only 0.7

ppm (Table 1), and the water seeping inside divers' masks had a pronounced hydrogen sulfide smell. The water was clear and we observed numerous dead benthic organisms, including polychaete worms, brachyuran crabs, mantis shrimp and hemichordates strewn about the bottom in various states of decay. Large patches of black material (that smelled of hydrogen sulfide when samples were returned to the vessel) and a filamentous material thought to be colonies of fungi or bacteria covered most of the bottom at each sampling station.

On 8 July a cruise was made to determine the seaward extent of low D.O. The water column was sampled along a transect from off the Brazos River mouth in 9-m depth to about 50 km offshore in 33-m depth (Fig. 1). Temperature, salinity and D.O. measurements made on water samples revealed a thermocline-halocline at about 10-m depth. Above this boundary the D.O. was > 4.0 ppm, but below the D.O. was < 2.0 ppm, and was < 1.0 ppm near the bottom at some stations (Fig. 5). We also collected samples at the "Southeast Lump", a rock formation about 19 km southeast of Freeport in about 18-m depth. Bottom D.O. was also about 1.0 ppm at this location. Thus an area of at least 400 km^2 off Freeport was affected by hypoxia.

Tropical storm Claudette's winds raked the upper Texas coast between July 23 and 26, and generated large offshore waves. On 30 July we sampled the offshore site and determined (by diving) that mixing had occurred only to 18.5-m depth. The bottom water at all stations was still hypoxic. The nearshore site was sampled 3 days later (2 August) and an average 3.0 ppm D.O. was recorded from bottom waters. It is not known exactly how long hypoxic conditions persisted at the offshore site after 30 July. A month later (31 August) the D.O. had risen to 2.5 ppm and continued to increase during the fall and winter. Like the onset of hypoxia, oxygenation of bottom waters apparently first occurred in relatively shallow water and spread seaward.

Effects of Hypoxia on the Benthic Communities

Until October 1978 the temporal trends of diversity and abundance were not synchronized at the two sites (Fig. 6). Once synchrony was established, the trends remained similar. Numbers of species and individuals were rather large during the 1978–79 winter, and increased to a spring peak in late March 1979. This was followed by a rapid decrease through May. During the hypoxic period (June-early August), both diversity and abundances were low. The numbers of individuals collected during June and July were approximately one order of magnitude lower than during the March peak abundance. Following disruption of hypoxia, there was a brief irruption as both numbers of species and individuals increased. At the height of this explosive increase of individuals, the total abundance was nearly equal to the March peak at each site. The post-hypoxic bloom lasted approximately 1 to 1.5 months and was followed by an equally rapid decline. The macrobenthic densities in the October–November period were as low or lower than during the hypoxic period. The increases in species and abundances beginning in December marked the onset of the winter-spring bloom.

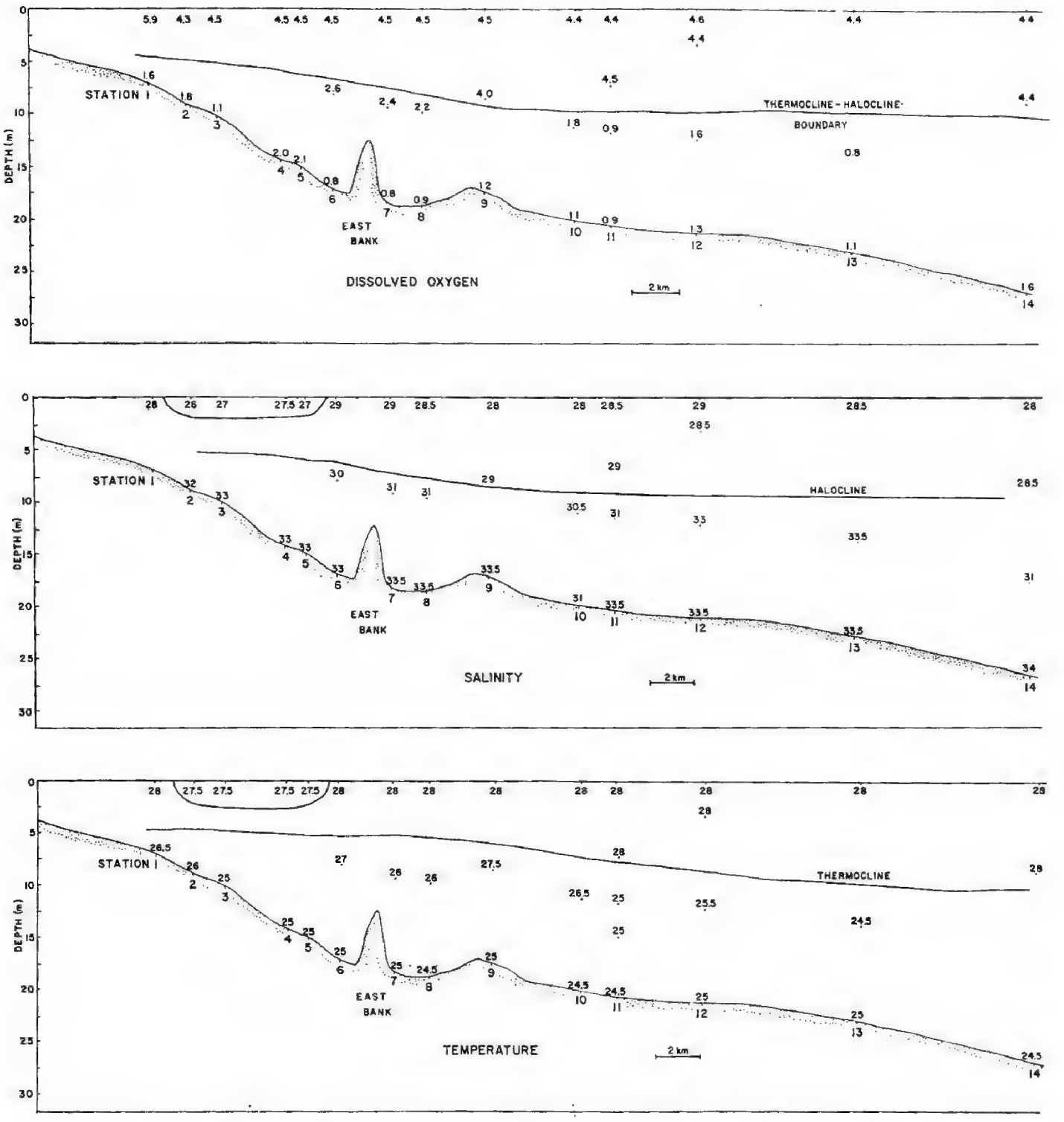


FIG. 5. Cross shelf temperature, salinity and dissolved oxygen profiles from data recorded on 8 July 1979.

Cluster analysis comparing species and months resulted in the months being separated into several clusters, and in both cases the hypoxic months were separated from most non-hypoxic months (Fig. 7). The nearshore site cluster containing hypoxic months also contained August 1978 and October 1979, both of which were months with very low diversity and abundance. In contrast the offshore hypoxic cluster contained only the hypoxic and immediate post-hypoxic months, May–November 1979.

Average monthly indices of diversity (H′) were high in the spring and late summer 1978 and spring 1979, and the trends were fairly well synchronized until hypoxia occurred (Fig. 8). As diversity and abundance declined in 1979,

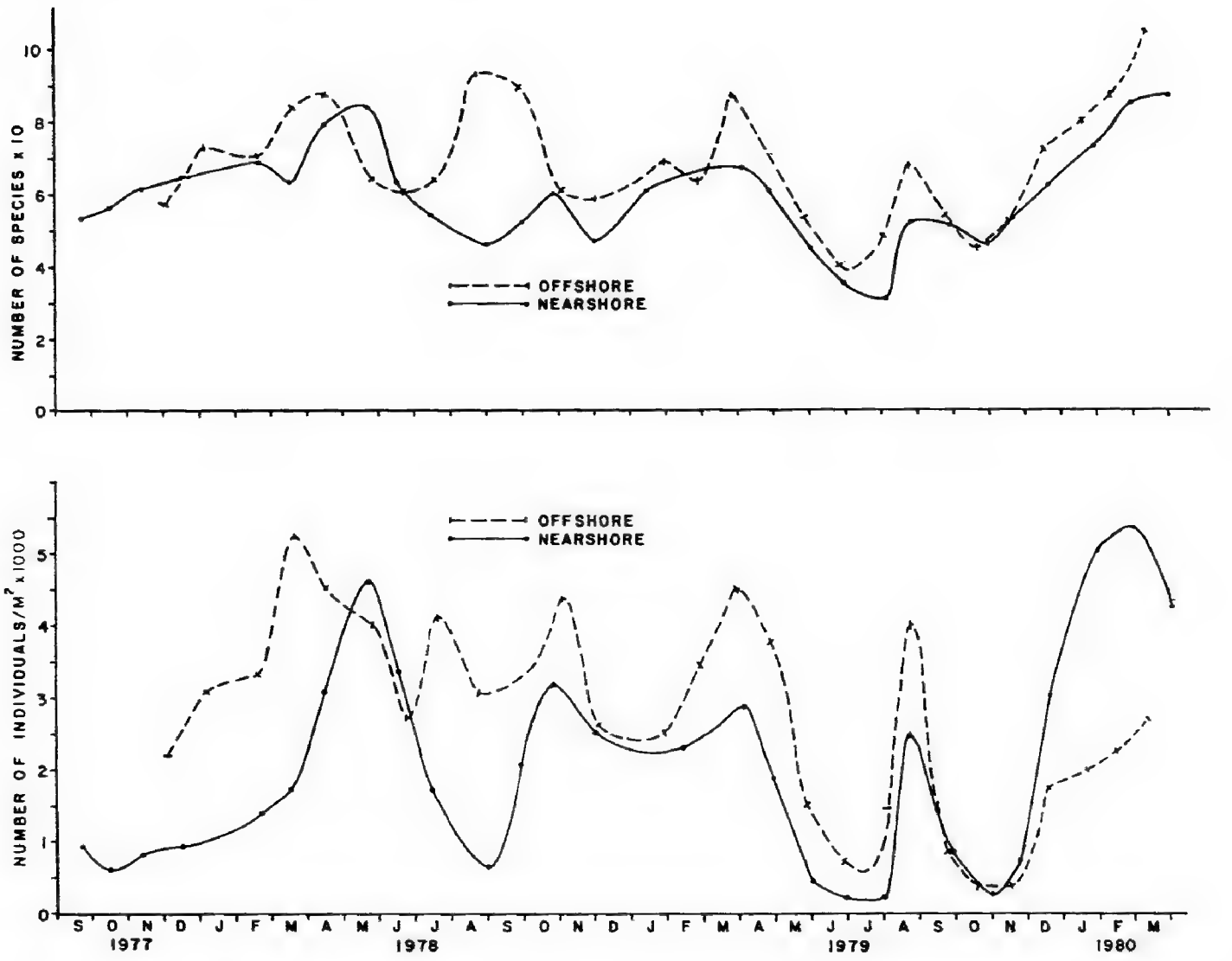

NUMBER OF SPECIES x 10
OFFSHORE
NEARSHORE
NUMBER OF INDIVIDUALS/M² x1000
OFFSHORE
NEARSHORE
S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M
1977
1978
1979
1980

FIG. 6. Comparison of the seasonal trends of total numbers of species and average numbers of individuals/m^2 collected at offshore and nearshore study areas.

the diversity indices also declined. At the offshore site, H′ oscillated once following hypoxia, increased in August–September and decreased in October–November, before beginning a continuous increase (Fig. 9). In contrast, the nearshore site H′ underwent several oscillations following the break-up of hypoxia and showed no signs of stabilizing by the end of the study. During the October–November period, the nearshore H′ was higher than offshore, the only time this reversal occurred.

ANOVA of H′ means indicated significant differences between months, and Duncan's multiple range test indicated there were considerable differences in the grouping of months between the study areas (Fig. 9). Offshore H′ changes appear to have been primarily related to season; winter months were not significantly different, nor were months before, during and after hypoxia (May–September), a time in which both diversity and abundance underwent extensive fluctuations. In contrast, rapid shifts occurred at the nearshore site, and the hypoxic months (June and July) were significantly different from pre- and post-hypoxic months.

ANOVA of mean log total abundance also indicated significant differences between cruises at both study areas. Duncan's multiple range test separated the cruises into several groups (Fig. 9). The winter-early spring periods were rela-

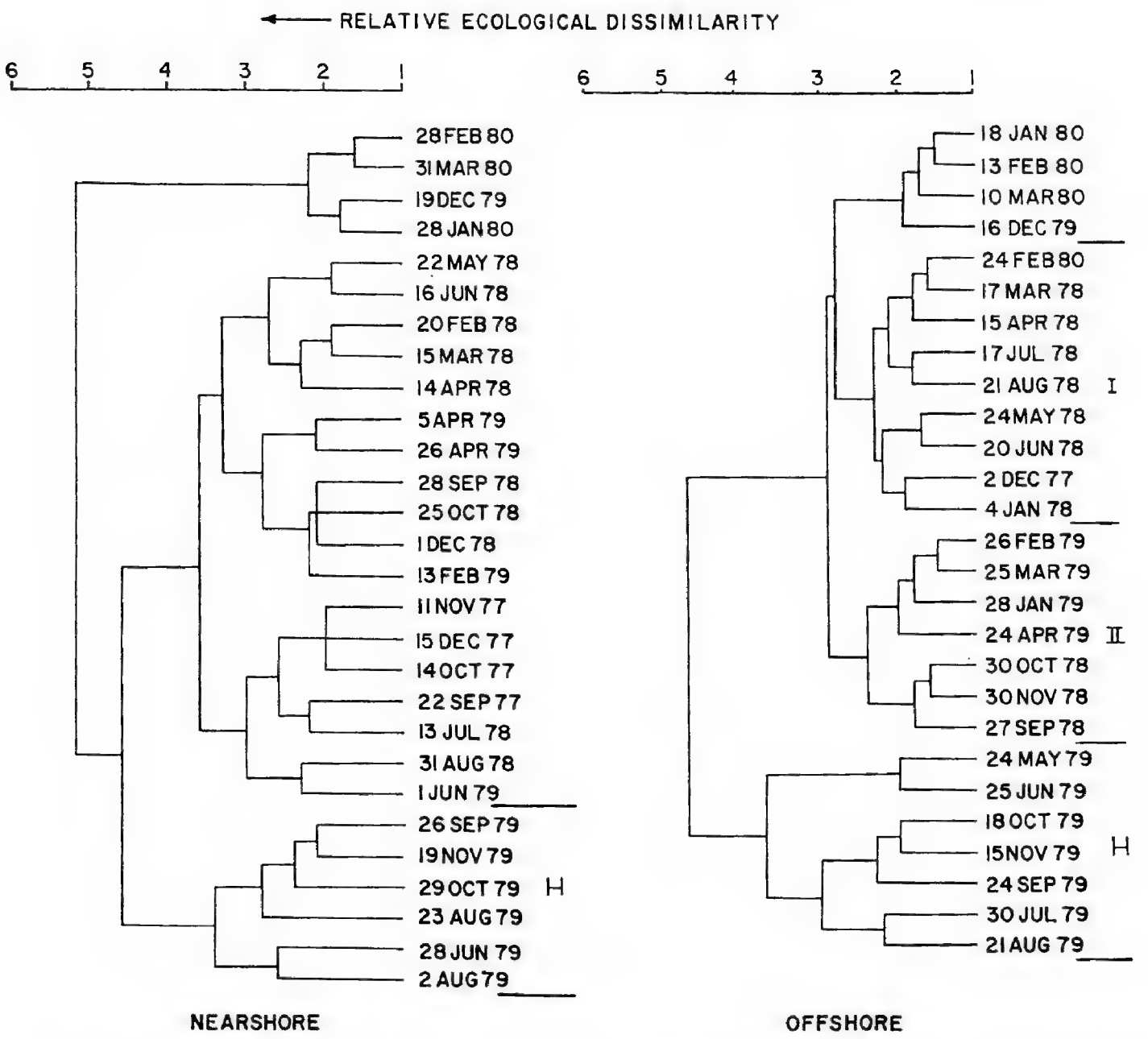


FIG. 7. Dendrograms showing the cruise groups formed by cluster analysis of offshore and nearshore data. I—period of polychaete dominance. II—period of amphipod dominance. H—hypoxic and post-hypoxic months.

tively stable, but between April and December at the nearshore site and between May and November at the offshore site there were rapid month to month changes in abundance.

The temporal changes in the percent composition of the dominant taxa show that Polychaeta was the dominant taxon (Fig. 10) when *Paraprionospio pinnata* populations were large (Fig. 11). At both sites the percentage of polychaetes began to decrease about November 1978 with a concomitant increase in amphipods and by spring 1979 amphipods equalled or exceeded polychaetes in abundance (Fig. 11). This trend was abruptly reversed when hypoxic conditions were manifest. The amphipods were virtually eradicated by late June and had only slightly recovered by March 1980. The increasing dominance of amphipods through March and April 1979 is also indicated in the time dendrogram of the offshore site. The larger cluster is divided into two sub-clusters, one

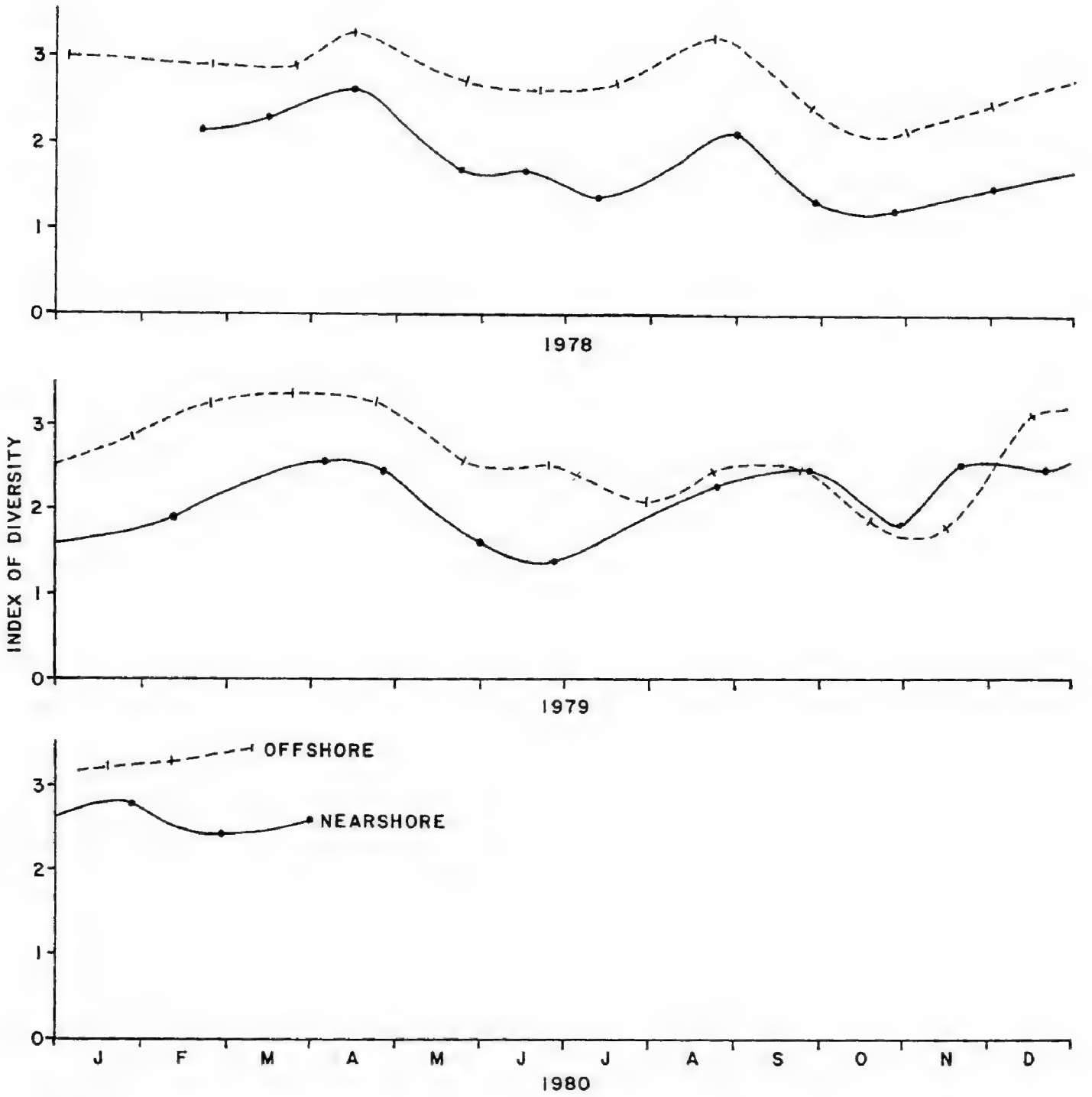


FIG. 8. Comparison of seasonal trends in the Shannon-Weiner diversity index at offshore and nearshore sites.

when polychaetes were dominant and one when amphipods were dominant (Fig. 7).

The third most abundant taxa were bivalves and nemerteans at the offshore and nearshore sites respectively (Fig. 10). Bivalves were usually abundant only in the July–August period when large numbers of juveniles were collected. These populations were quickly reduced, probably by predation and/or natural death, and did not appear to be affected by hypoxia. The *Abra aequalis* population irrupted at the nearshore site beginning in December 1979. Nemerteans (principally *Cerebratulus lacteus*) were present in relatively small numbers throughout the study and did not appear to be affected by hypoxia.

Several species, selected because they were among the numerical dominants either overall or in their taxa at one or both sites, further illustrate the effects of hypoxia on members of the community. The polychaete *Paraprionospio pin-*

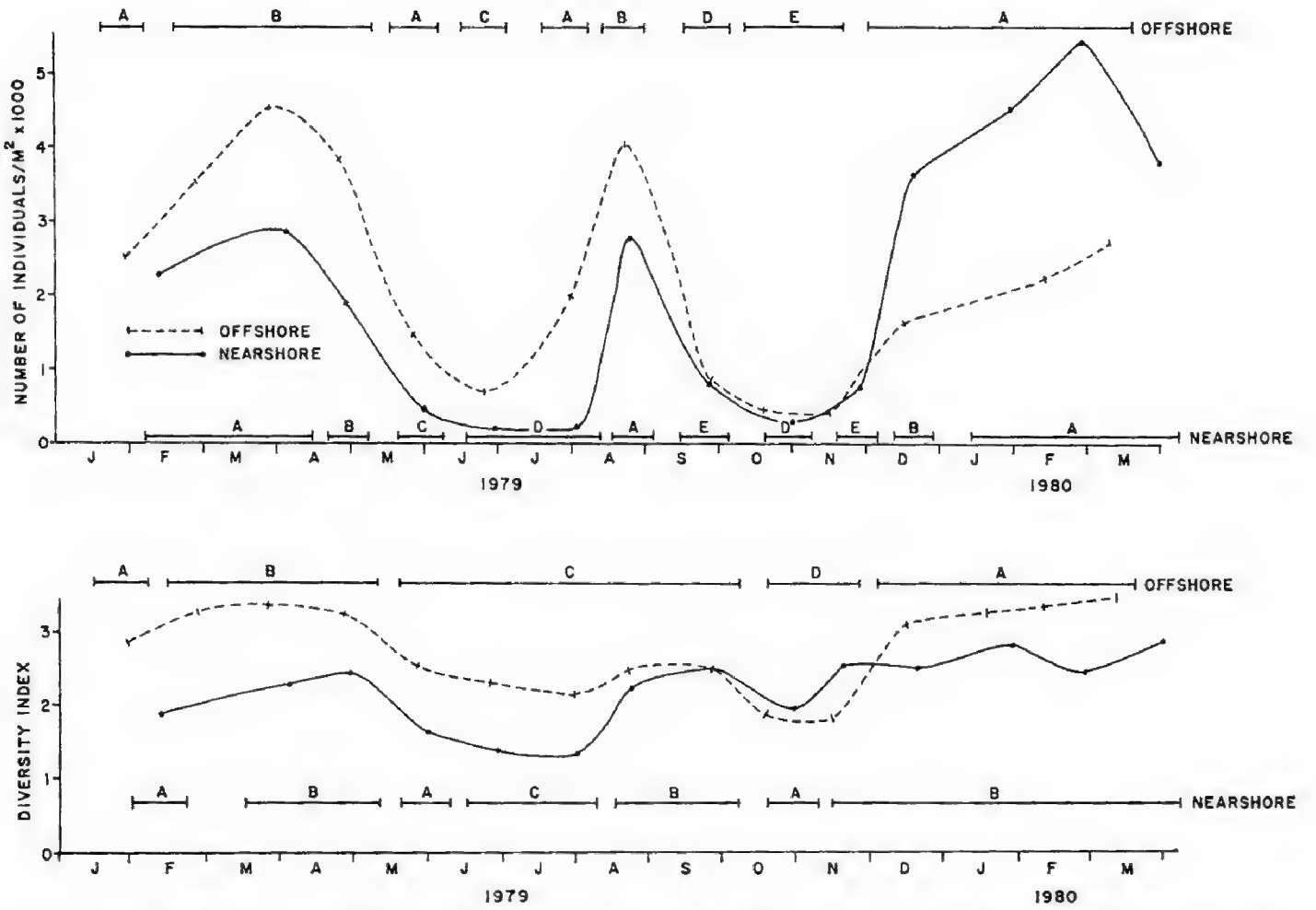


FIG. 9. Results of Duncan's multiple range test performed on mean log transformed total abundance and mean Shannon-Weiner diversity index (H′) compared with seasonal trends of abundance and H′. I-bars with the same letter bracket denote months in which means were not significantly different.

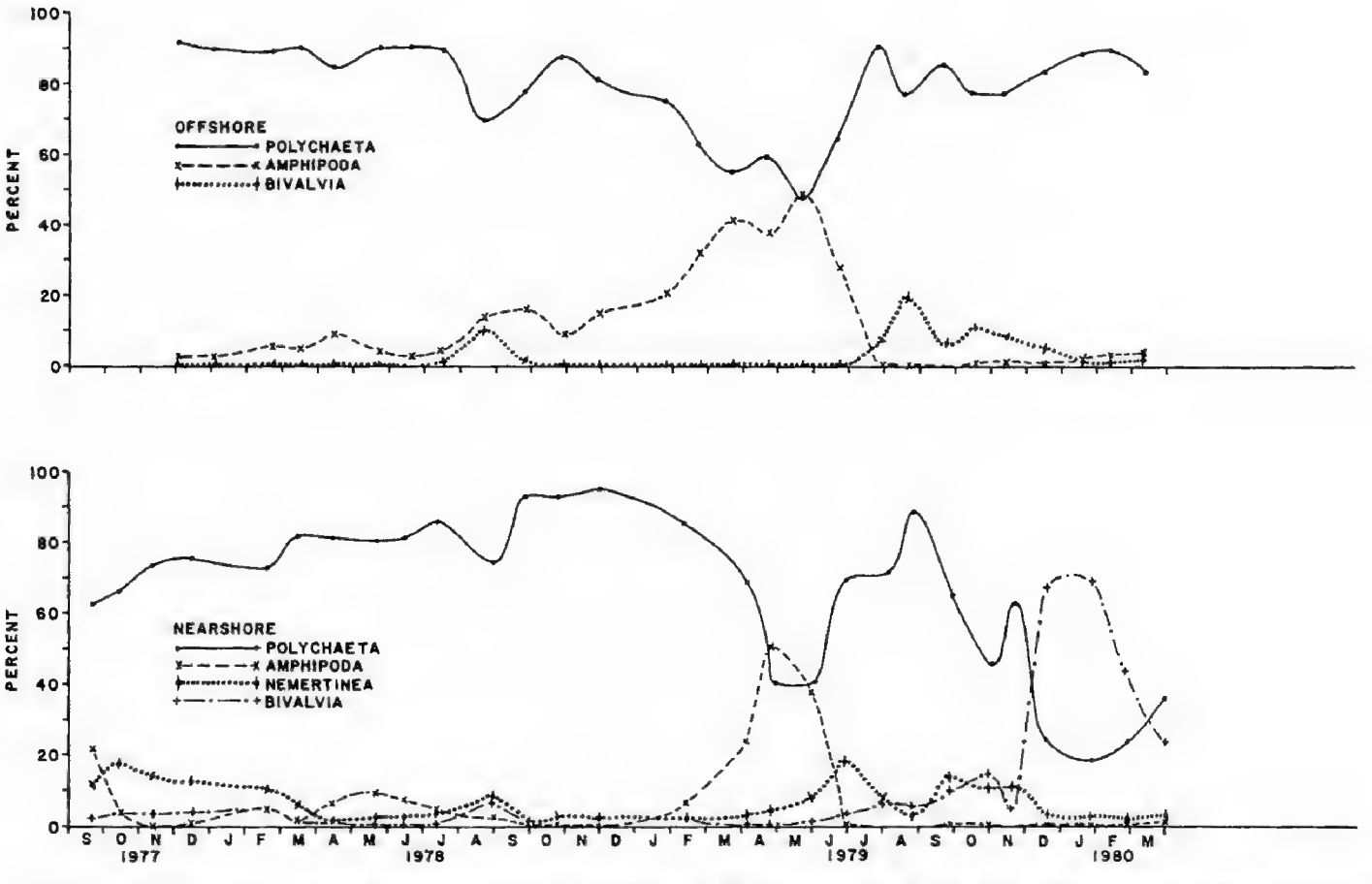


FIG. 10. Comparison of the seasonal trends of dominant taxa at the offshore and nearshore study areas.

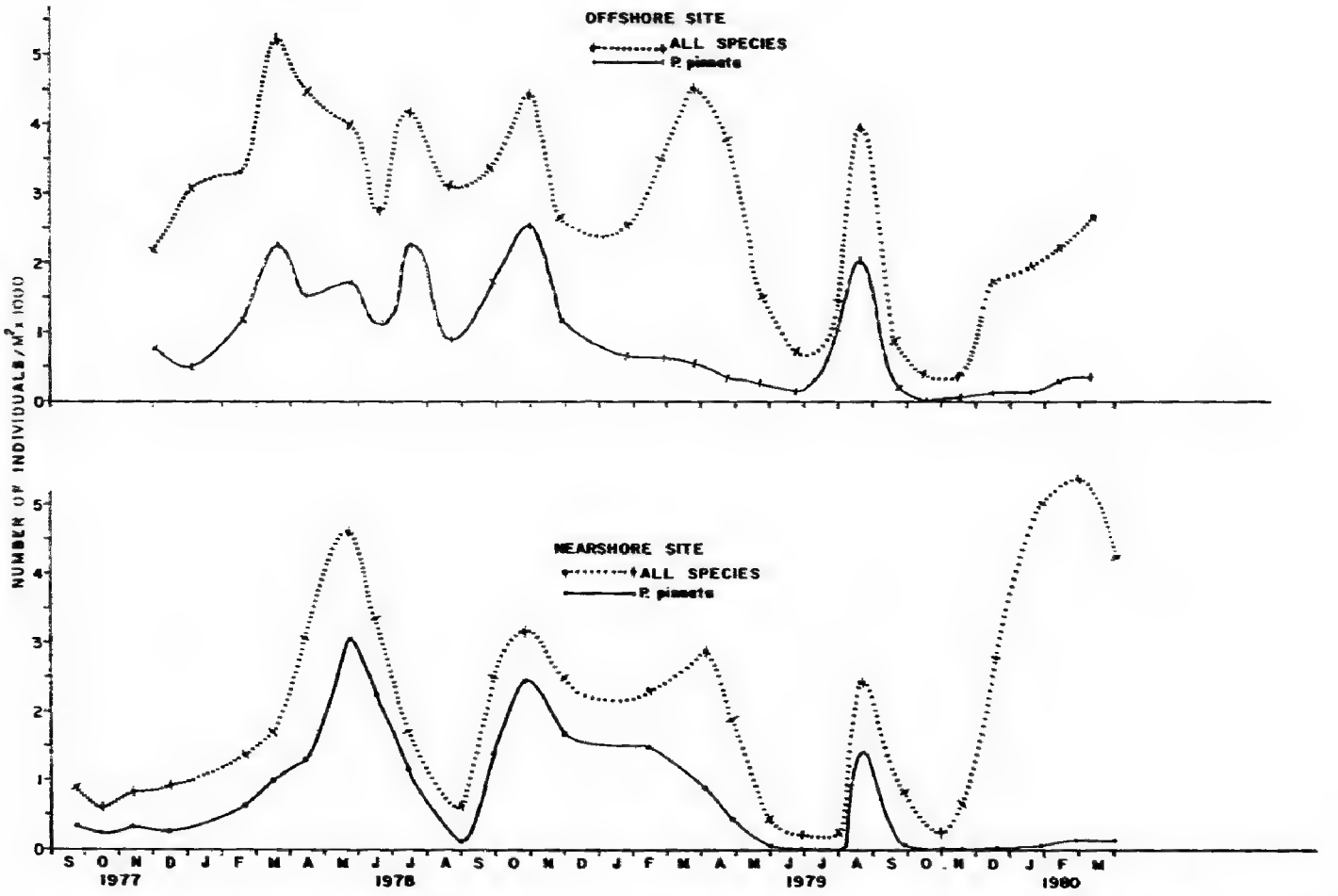
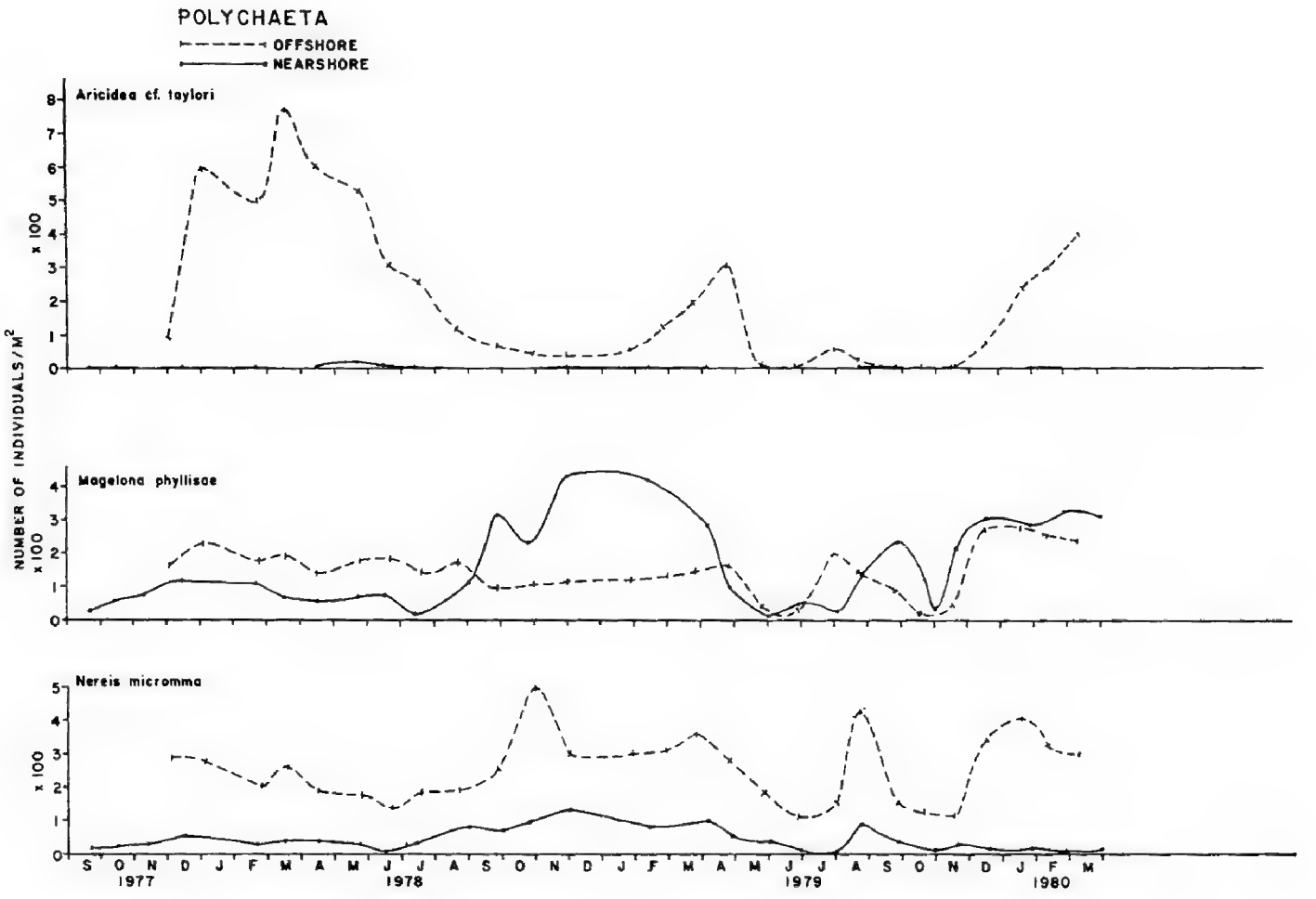

OFFSHORE SITE
ALL SPECIES
P. pinnata
NEARSHORE SITE
ALL SPECIES
P. pinnata
NUMBER OF INDIVIDUALS/M² x 1000
S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M
1977
1978
1979
1980

FIG. 11. Comparison of *Paraprionospio pinnata* and total benthic abundance at the offshore and nearshore study areas.

nata, because of its great numerical dominance, was very influentual in determining the sizes of total monthly abundances at both sites during the first year of study (Fig. 11). At the nearshore site, this trend persisted through October 1979, after which the massive set of *Abra aequalis* (which primarily occurred at three stations) caused this clam to become dominant. However, at the offshore site, *P. pinnata* dominance declined after November 1978 when the amphipod ascendency began. This species had low population densities through the hypoxic period, contributed greatly to the post-hypoxic irruption, and then declined to very low numbers during the remainder of the study period. The nearshore population appears to have been the most severely affected during hypoxia, decreasing to almost zero.

Populations of other dominant polychaete species varied irregularly throughout the study period and displayed no tendency to attain common peak abundances seasonally. All, however, decreased to very low densities during the hypoxic period (Fig. 12). Some species (i.e. *Nereis micromma*, *Magelona phyllisae*, *Armandia maculata*) contributed to the post hypoxic irruption, while others (i.e. *Prionospio cristata*, *Mediomastus californiensis*, *Lumbrineris verrilli*, *Aricidea taylori*) continued to have low populations until the beginning of the winter–spring increase in November 1979.

Amphipods were the group most severely impacted by hypoxic conditions (Fig. 13). The dominant amphipod species displayed a pronounced seasonality in prior years, with largest population densities in the spring and lesser blooms



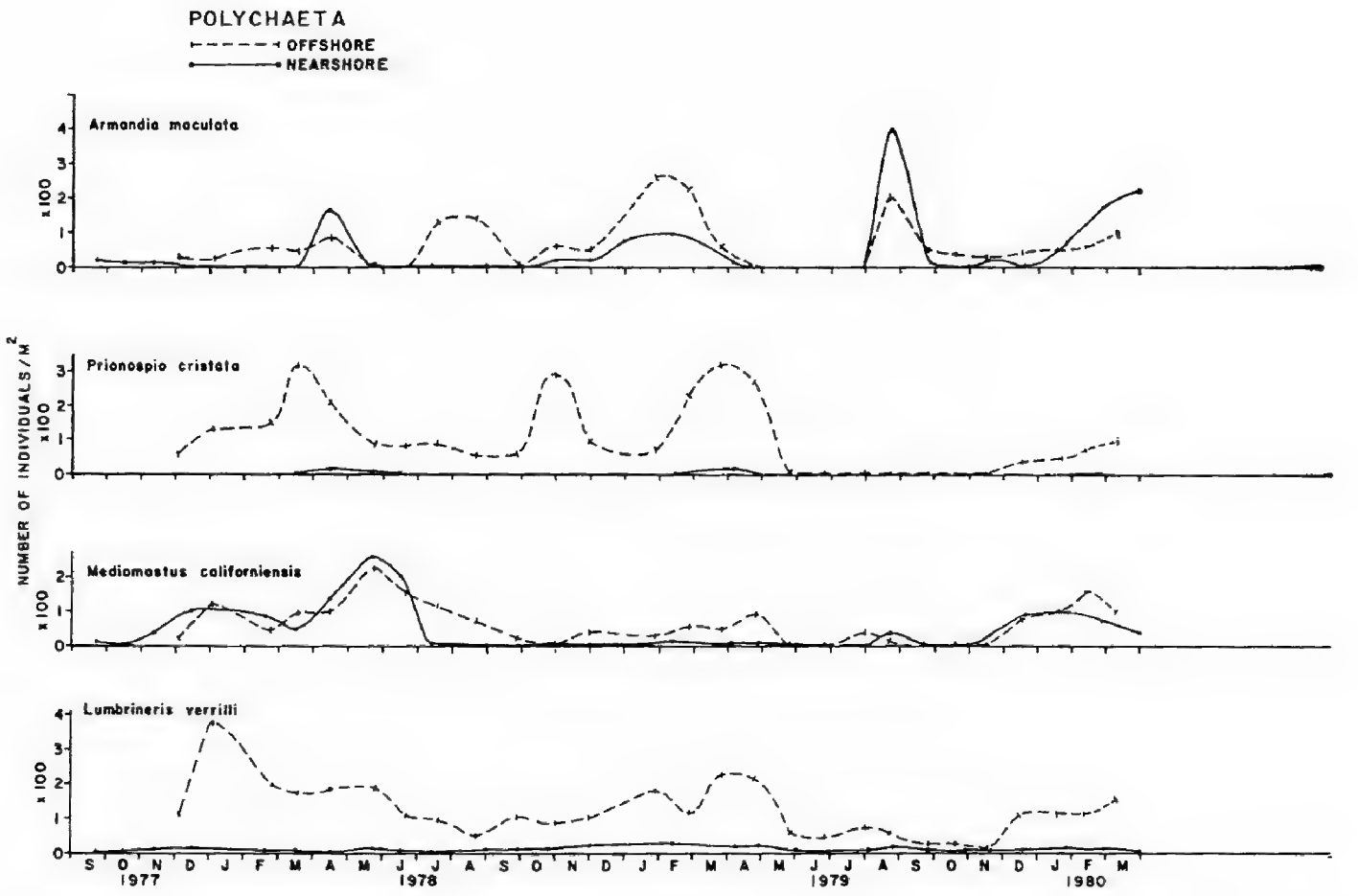


FIG. 12. Comparison of seasonal trends of populations of selected polychaete species at the offshore and nearshore study areas.

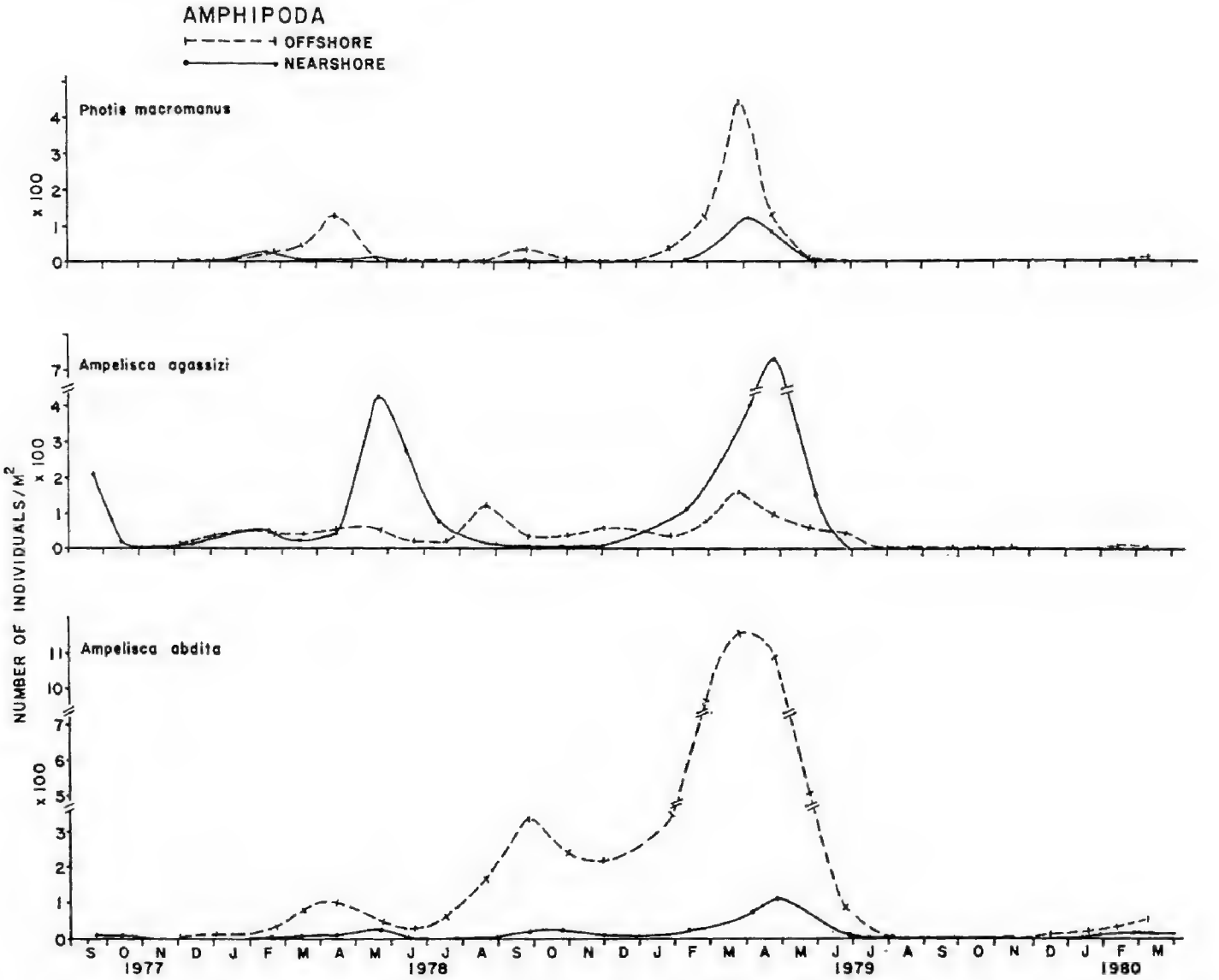


FIG. 13. Comparison of seasonal trends of populations of selected amphipod species at the offshore and nearshore study areas.

in the fall, and with each peak larger than the one preceding. The spring 1979 peaks of all three species were much larger than the spring 1978 peaks, which made the subsequent decline even more dramatic. All three species were virtually eliminated from the benthic assemblages by July, the second month of hypoxic conditions, and none had recovered by March 1980.

Dominant bivalves (Fig. 14) did not appear to be affected by hypoxia at all. Dominant species displayed a consistent trend of late summer abundance, usually in August, and there is no evidence that hypoxia altered this seasonal pattern. The rapid increase of *Abra aequalis*, though, suggests that some event mid–1979 caused high levels of reproduction. The number of bivalve veligers collected increased steadily from October through December then abruptly disappeared (Park and Minello 1980). The population of young *Abra* appeared concurrent with the maximum population of veligers.

Effects of Hypoxia on the Fauna of East Bank

We periodically examined the fauna of East Bank, a rocky structure lying between the nearshore and offshore study areas (Fig. 1). This bank rose from

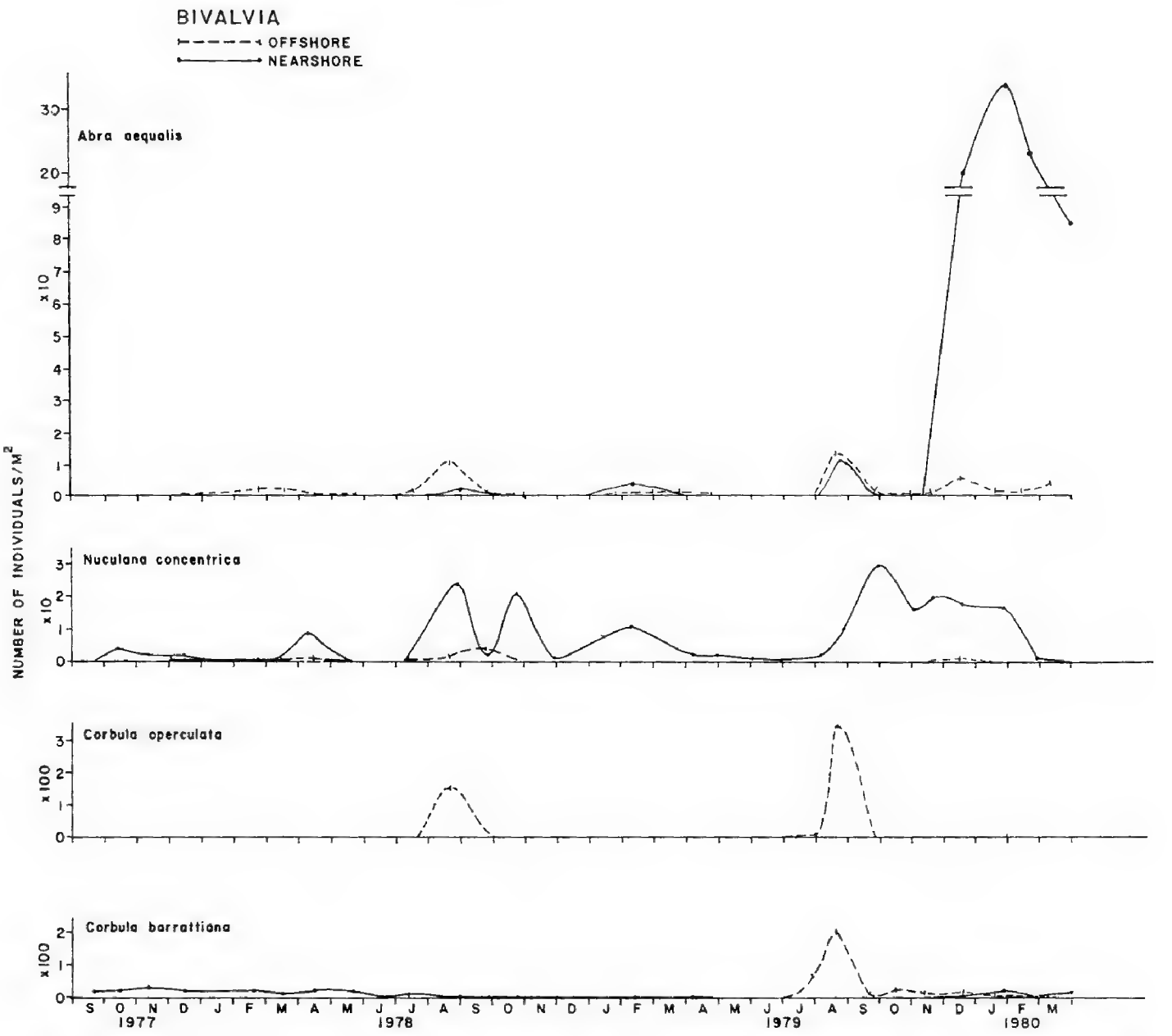


FIG. 14. Comparison of seasonal trends of populations of selected bivalve species at the offshore and nearshore study areas.

17.5-m depth to a crown depth of 12 m. Visits to the bank were irregular because of usual poor visibility (< 1 m), and no quantitative measurements were made. However our observations further illustrate the severity of hypoxia.

Prior to 28 June (when we observed dead infauna at the nearshore site) the bank had an apparently healthy assemblage of sea whips (*Leptogorgia* sp.), solitary corals (*Astrangia astraeiformis*), sea urchins (*Arbacia punctulata*), mollusks, crabs and associated reef fish. However, on 28 June we observed considerable mortalities. Every sea urchin was dead and mostly decayed. Many sea whips were missing sections of the colony and the internal skeletons were exposed. All corals collected or observed *in situ* appeared dead. Hermit crabs, which were widely scattered prior to 28 June, were clustered at the edges of the highest rock slabs and many were moribund or dead. The large gastropod mollusks observed (*Murex fulvescens*, *Pleuroploca gigantea* were sluggish and retracted very slowly when picked up. The only fish seen were three toadfish; the normal component of reef fish was not present.

East Bank was again inspected on 30 July after the passage of Tropical Storm Claudette, and 3.7 ppm D.O. was measured. The invertebrate fauna had suffered considerable mortalities in addition to those observed on 28 June. In particular, we noted that numerous empty ark clams (*Arca* cf. *imbricata*) were scattered about the rocks. However, the reef fish population had apparently returned to normal.

Subsequent examination of the bank has indicated that the most severely affected species will probably require considerable time to recover. No urchins were seen by the end of the study (and none were observed until December 1980). A few small, young sea whip colonies appeared by late summer of 1980. Several new coral colonies were noted by early 1980, which suggested a more rapid comeback for this species.

DISCUSSION

The benthic communities in the two level bottom study areas were comprised of different assemblages of organisms. Even the species that co-occurred at the two sites rarely had the same numerical rank. These differences and the observed seasonal trends are controlled by a combination of abiotic and biological factors. Abiotic factors, i.e. substrate composition, depth (temperature and salinity stability, D.O. availability), seasonal temperature and salinity trends, and biological factors, i.e. competition for food, space, etc., and predation, exert their influence on a more or less regular basis. While any given species may be reduced by unfavorable temperature, salinity or substrate characteristics, or the presence of large populations of predators, several species still manage to attain large populations and the overall community density usually remains relatively high. Protracted hypoxia, on the other hand, generates a more uniform stress on the established community. While some organisms can tolerate anoxic conditions for a few hours and others can survive hypoxic conditions for limited periods of time because of anaerobic metabolic pathways, survival in such adapted species is usually of limited duration (Jones 1972, Newell 1973, Mangum and Van Winkle 1973). Species inhabiting reduced soft bottoms and those less active have higher resistance to hypoxia (Theede *et al.* 1969), but there still may be a 5-fold decrease in metazoan biomass when D.O. decreases to 0.7–0.3 ppm (Rosenberg 1977). Furthermore, the upper Texas coast lies in the subhumid climatic zone where precipitation and evaporation are balanced, or there is a slight rainfall surplus (Thornthwaite 1948), and floods are not a common occurrence. Hypoxic conditions therefore probably occur infrequently and the species are not provided much opportunity for tolerant members to be selected.

In 1979 the effect of low oxygen concentrations at the nearshore, and possibly the offshore, study area was exacerbated by the presence of hydrogen sulfide in the bottom of the water column and sediments. Hydrogen sulfide, a poison to most organisms, is produced by sulfate reducing bacteria which become dominant only after aerobic metabolism has depleted oxygen in the water. The sudden occurrence of hydrogen sulfide and oxygen deficient water can cause mass mortalities (Theede *et al.* 1969).

Hypoxia may have occurred in 1978 at the nearshore site. The seasonal trends of both diversity and total abundance may be divided into two phases (Fig. 6). Prior to October 1978 the trends at the two sites were asynchronous, and since then have been essentially synchronous. The cause of asynchrony is not known, but apparently was established prior to the start of our study. Synchrony was established after nearshore diversity and abundance declined rapidly in summer 1978, culminating in a late August nadir. This suggests a hypoxic event. However, H′ trends at both sites increased during this period (Fig. 8), and these data do not support a nearshore hypoxia theory. Because offshore and nearshore diversity and abundance trends were synchronized shortly after the event, whatever its cause, it may have also caused the synchrony.

Hypoxia and associated hydrogen sulfide in 1979 may have originated locally or may have been transported into Texas waters from Louisiana by westward flowing water masses. The latter is suggested by the fact that preliminary fisheries data indicate record low catches of fish and shrimp were made along the Texas coast from Sabine Pass to Matagorda Bay during the hypoxic period. Whatever the source several events occurred during our study that paralleled the sequence of events postulated by Falkowski, Hopkins and Walsh (1980) as causing anoxia in New York Bight, viz: large runoff volumes, high organic load, phytoplankton bloom and stratification. Large volumes of water were discharged from local rivers and the Mississippi River in the spring. High organic (PO_4, NO_3, Si) and chlorophyll *a* values were recorded in surface waters in May (Slowey 1980). Phytoplankton samples were first collected in early June, and at that time a phytoplankton bloom (ca. 1500 cells/ml), comprised mostly of diatoms, was occurring in surface waters (Loeblich and Matthews 1980). On 28 June we discovered dead invertebrates on the bottom at the nearshore site, and on 29 June Slowey (1980) found high phaeophytin *a* (a degradation product of chlorophyll *a*) levels and dissolved organic levels at or below detection levels. Phytoplankton densities decreased by about two orders of magnitude between June and August while nitrates and silica increased to high levels in bottom waters by August (Loeblich and Matthews 1980, Slowey 1980).

The preceding data suggest the following scenario to account for the hypoxia. High spring runoff carried dissolved organics into coastal waters. A diatom bloom ensued, probably peaking in May and began to decline as nutrients were exhausted, hence the high phaeophytin *a* values in June even though phytoplankton densities were still high. By late June, calm weather and fresh water had combined to produce intense stratification which inhibited diffusion of oxygen from the surface. At the same time, dead phytoplankton accumulating on the bottom were attacked by microorganisms, further reducing the oxygen tension, and finally sulfate reducing bacteria generated hydrogen sulfide. As D.O. levels decreased, the more susceptible benthic organisms perished and decomposition of their bodies undoubtedly added to oxygen depletion. The microorganisms may have produced the filamentous patches observed on the bottom. They were very similar to patches seen by one of us (Harper) in 1974 at King Harbor, Redondo Beach, California, following decay of a red tide bloom.

We believe the macrobenthic kill began about the last week of June. The dead, but intact, invertebrates we observed had not been dead long, and the fact that Slowey (1980) found no dissolved organics the day following our observations suggests decomposition was a recent process. Hypoxic conditions continued at least until 21 July when Chittenden (1981) collected virtually no nekton between depths of 10 and 27 m. Waves over 2 m in height generated by Tropical Storm Claudette occurred between July 22 and 27 and undoubtedly disrupted hypoxia at the nearshore site. These waves mixed the water to 18.5 m at the offshore site and probably contributed to the breakup of hypoxia at that site soon after.

Percentages of living and dead organisms cannot be estimated because our samples were preserved immediately upon collection. This procedure may have resulted in higher apparent abundances than actually existed if dead, but undecomposed organisms were collected. During a hypoxic event off New Jersey, Garlo, Milstein and Jahn (1979) estimated 2% mortalities in July and 20% in September 1976, using responses of organisms to stimuli as the live/dead criterion. On the basis of our quantitative soft bottom data and rock reef observations, echinoderms and amphipods appeared to be most affected by hypoxia, and polychaetes and bivalves the least. This is in general agreement with the results of McErlean *et al.* (1972), Simon and Dauer (1977) and Garlo *et al.* (1979).

The rate of recovery of the taxa after hypoxic conditions ended also differed. A few species of polychaetes maintained low populations at the offshore site during the hypoxic period (i.e. *Nereis micromma*, *Lumbrineris verrilli*) and increased in abundance immediately after hypoxia abated. Other species (i.e. *Paraprionospio pinnata*, *Magelona phyllisae*) populations were greatly reduced during hypoxia, yet contributed to the post-hypoxic irruption. We classified most post-hypoxic individuals of polychaetes as young, suggesting larval recruitment as the principal means of population increase. Migration of adult polychaetes has been suggested as a mechanism for repopulating defaunated areas (Dauer and Simon 1976), but more recent work (Santos and Simon 1980a) has indicated that adult migration occurs principally among crustaceans and that larval transport is the most important means of polychaete repopulation.

Amphipods brood their young and do not have planktonic larval stages. Adults must, therefore, depend on their relatively limited swimming ability or transport by some object ("rafting") for dispersion. If hypoxia was as extensive as we believe, the reproductive base of the amphipods was greatly reduced and probably accounts for the very slow recovery of amphipod populations.

The bivalves, which displayed a tendency to attain peak population in August (Fig. 14), did not appear to be greatly affected by hypoxia. It is probable that the larvae were either in surface waters during hypoxia, or were transported into the study areas and available for recolonization after hypoxia ended.

The trends of total abundance and numbers of species were similar at the two sites during 1979 and early 1980. Diversity index trends were not. H′ oscillated repeatedly at the nearshore site during and immediately following

hypoxia, and this is reflected in the lack of month to month continuity in Duncan's multiple range test results (Fig. 9). The oscillating response of H′ after hypoxia ended indicates ecological instability and would be expected in an area subjected to such disturbances periodically (Holling 1973).

Santos and Bloom (1980) proposed a working definition for ecological stability: "the ability of a system once perturbed to return to its previous state." In the system they studied, summer defaunations occurred in each of four years. After the third defaunation the system was declared unstable because the community shifted to a new stable point based on pre-defaunation data, i.e. old dominants were replaced by new dominants (Santos and Simon 1980b). The nearshore site appears to fall in this category. Prior to hypoxia, *Paraprionospio pinnata* dominated the assemblage until amphipods increased in abundance. After hypoxia, a series of short term dominants replaced one another sequentially (Harper and McKinney, in MS).

The offshore site H′ was much less oscillatory, which was reflected in the longer month-to-month periods of no significant difference as determined by Duncan's multiple range test. The offshore site was also more stable in terms of recovery of dominant species after hypoxia ended (Harper and McKinney, in MS).

The results of this study also emphasize another very important point. *Adequate* baseline data must be collected before the effect of human activities on the environment can be determined. If brine discharge (which was the reason for initiating this study) had begun just before or concurrent with the onset of hypoxia, the resultant mortalities would most certainly have been blamed on the brine. Local fishermen were convinced that discharge operations had begun until they were told of the low amounts of D.O. in the water. In making sound coastal management decisions it is essential to distinguish between naturally occurring mortalities and those caused by human activities.

ACKNOWLEDGMENTS

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VARIABILITY OF ZOOPLANKTON TOWS IN A SHALLOW ESTUARY

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ABSTRACT

Short-term variability in the zooplankton of a shallow estuary with minimal tidal fluctuations in the northwestern Gulf of Mexico was examined at one station on April 13 through 15, 1976. Densities were estimated from three replicate oblique tows taken every four hours over the 44-hour study period. Counting and subsampling error was not significant compared with replicate tow variability, and replicate tow variability was small compared with the variability among sampling times. Overall densities were large during the night compared to the day and the greatest variability in replicate tows occurred during both sunrise sampling times.

INTRODUCTION

Estuarine systems in the northwestern Gulf of Mexico are frequently characterized by minimal tidal fluctuations and extremely shallow basins. The short-term (hours-days) variability in density estimates from zooplankton tows in other types of estuaries has often been associated with tidal fluctuations and in some cases with the diel vertical movement of organisms in relatively deep bay waters (Hopkins 1963, Pillai and Pillai 1973, Sameoto 1975, Trinast 1975, Lee and McAlice 1979, Youngbluth 1980). Although the number of zooplankton studies conducted in coastal estuaries of the northwestern Gulf has increased steadily in the past 2 decades (Matthews 1980), work on sampling variability in these areas has not been published. This study was designed to examine the extent of short-term variability of density estimates from zooplankton tows taken in West Bay, Texas (maximum depth of 1.8 m), and to determine the relative importance of factors contributing to this variability.

The short-term variability in results obtained from zooplankton net tows taken at a fixed station can be divided into three components each with several possible causal factors:

1) Variability over a short period of time (hours-days).
   a. Movement of water past a sampling point introducing new populations (tidal flow, currents).
   b. Vertical migration of organisms if tows do not cover the entire water column.
   c. Biological changes in populations (growth, mortality).
   d. Differential avoidance of nets due to varying light intensities.

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2) Variability at one specific time.
   a. Small scale horizontal patchiness.
   b. Vertical stratification of the zooplankton combined with variations in sampling depth.
   c. Flowmeter inaccuracies.
   d. Variability in net clogging.
3) Variability introduced in the laboratory.
   a. Subsampling error.
   b. Counting error.

The sampling scheme and data analysis used in this study were designed to examine the relative importance of these three error components. Causal factors for the observed variability are considered and methods for reducing this variability are suggested.

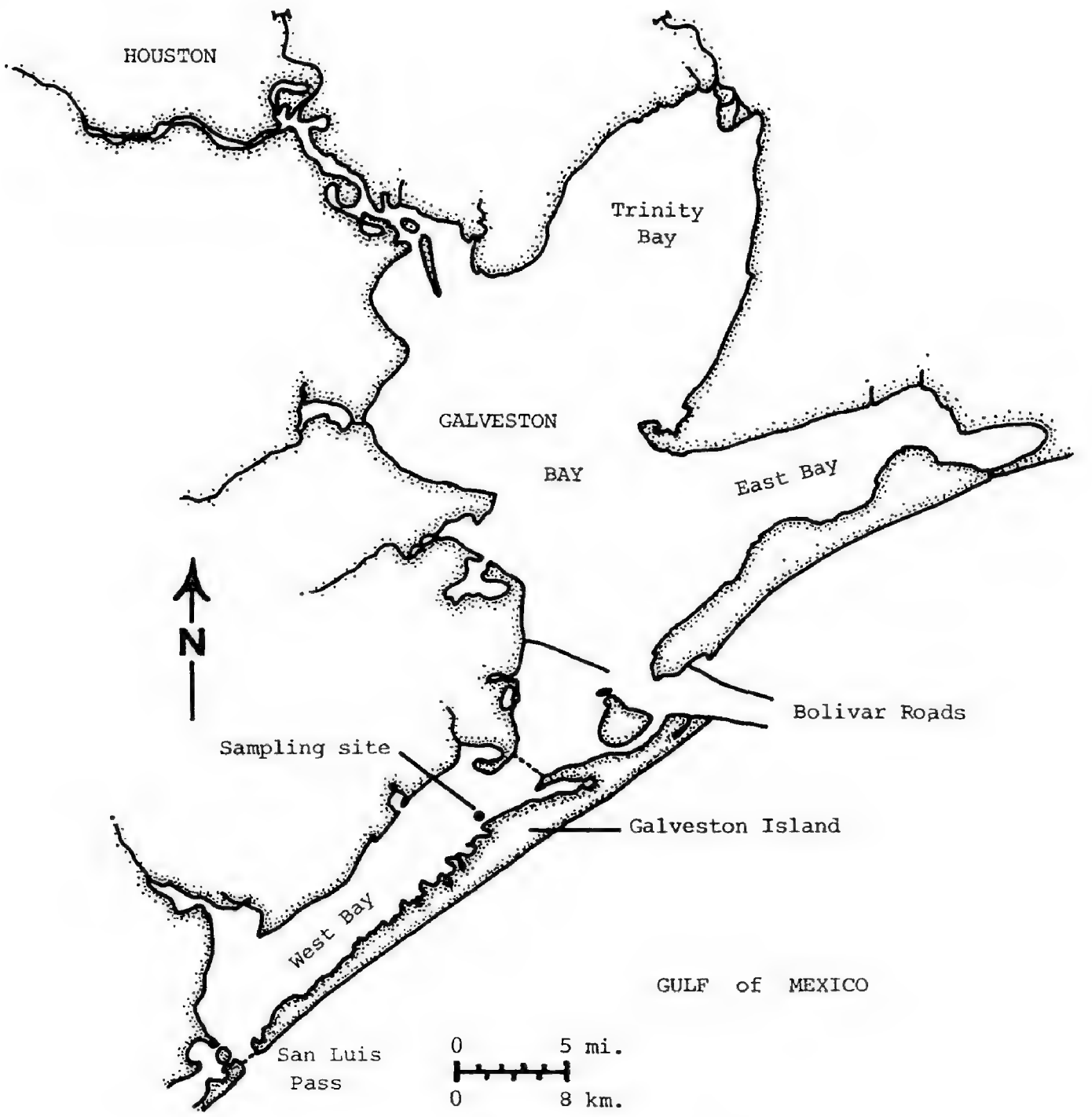

FIG. 1. Map of the study area.

MATERIALS AND METHODS

A single sampling station was established in West Bay, a shallow polyhaline bay in the Galveston Bay System (Fig. 1). The station was located midway between San Luis Pass and Bolivar Roads, the two major inlets connecting the bay system with the Gulf of Mexico. Tidal fluctuations in this area are small, ranging from 0.3 to 0.5 m (Pullen, Trent, and Adams 1971).

Intensive zooplankton sampling was conducted over a 44-hour period from April 13 to 15, 1976. Three replicate oblique tows were taken every 4 hours over the study period (36 tows). The 12 sampling times were numbered sequentially beginning with sampling time 1 at 2100 hours on April 13 and ending with sampling time 12 at 1700 hours on April 15. Each set of three tows was taken within 45 minutes of the recorded sampling time. The sampling gear consisted of a 0.5 m conical net made of 241 μm mesh Nitex. A General Oceanics digital flowmeter was mounted in the center of the net mouth. Five-minute oblique tows were taken at approximately 1 m/sec from a 4.9-m (16-ft) skiff, and an average of 36 m^3 of water was filtered per tow. During the tows the net, lowered and raised by hand, reached to within 0.5 m of the bottom. Tows were taken in a wide circle to eliminate any influence of propeller turbulence from the outboard engine. The depth of the water at our station was approximately 1.8 m at mean tide level.

Water temperature, salinity, and turbidity were measured from surface samples taken at each of the 12 sampling times. Tide data were obtained from hourly readings taken by the U.S. Weather Bureau at Pier 21 in Galveston Channel and were corrected with a lag time of 2.25 hours for the distance to our sampling station. Data on wind speed were obtained from measurements recorded at the Galveston Airport Weather Station located approximately 7 km from our sampling site.

A 5-ml Hensen-Stempel pipet was used in the laboratory to take three subsamples from each sample collected. The volumes of the samples were adjusted with tap water according to the amount of water filtered during the tow, so that every 5-ml subsample represented 0.25 m^3 of water filtered. The 108 subsamples were analyzed in a random order to prevent a biased count of individuals. Densities of four categories of organisms were recorded: total zooplankton, *Acartia tonsa*, *Pseudodiaptomus coronatus*, and barnacle nauplii (*Balanus* spp.). Copepodid stages were combined with adults in all counts of copepods. Few copepod nauplii were captured in our net.

A nested analysis of variance (Hicks 1973) on log transformed densities was used to analyze the data. The log transformation appeared to adequately normalize the densities and reduce the positive relationship between the mean and the variance present in the untransformed data. Variability among the 12 sampling times was tested with replicate tow variability (tows taken at one time), and replicate tow variability was tested with the laboratory variability. Duncan's multiple range test was used to compare mean densities at the 12 sampling times. Confidence intervals based on subsampling and coefficients of variation were calculated from untransformed data.

RESULTS

The variability among the 12 sampling times was high in relation to the replicate tow variability. F values calculated for sampling times in the analyses of variance for all four categories of organisms were highly significant (Table 1). Over the sampling period large numbers of organisms were consistently captured during the night at high tide, and relatively few organisms were caught during the day at low tide. This pattern was exhibited to various extents by all groups of organisms examined (Fig. 2 and 3). Mean densities for total zooplankton, *Acartia tonsa*, and *Pseudodiaptomus coronatus* from the three daylight time periods on April 14 were significantly lower (5% level) than those of all other time periods (Table 2). Differences among mean densities

TABLE 1

The analysis of variance results calculated from log transformed densities for the four categories of organisms examined.

Source of variation	df	SS	F	P
Total Zooplankton				
Total	107	75.49		
Sampling times	11	60.54	8.96	$\leq$ 0.0001
Replicate tows	24	14.74	214.02	$\leq$ 0.0001
Laboratory error	72	0.21		
Acartia tonsa				
Total	107	96.89		
Sampling times	11	73.23	6.83	$\leq$ 0.0001
Replicate tows	24	23.40	270.28	$\leq$ 0.0001
Laboratory error	72	0.26		
Barnacle nauplii				
Total	107	108.45		
Sampling times	11	99.18	31.73	$\leq$ 0.0001
Replicate tows	24	6.82	8.35	$\leq$ 0.0001
Laboratory error	72	2.49		
Pseudodiaptomus coronatus				
Total	107	284.20		
Sampling times	11	243.83	14.88	$\leq$ 0.0001
Replicate tows	24	35.74	23.19	$\leq$ 0.0001
Laboratory error	72	4.62		

of barnacle nauplii for the 12 time periods were more complex. Although small variations in surface water temperature were apparent, surface temperatures and salinities were generally similar throughout the study period and did not appear to be related to changes in density of the organisms (Table 3). Increased densities of organisms during the daylight hours of April 15 compared to the daylight hours of April 14 coincided with increased wind speed and turbidity.

Replicate tow variability (variability within time periods) was high in relation to the laboratory error. Analysis of variance results for all four categories of organisms examined indicated highly significant F values for replicate tows

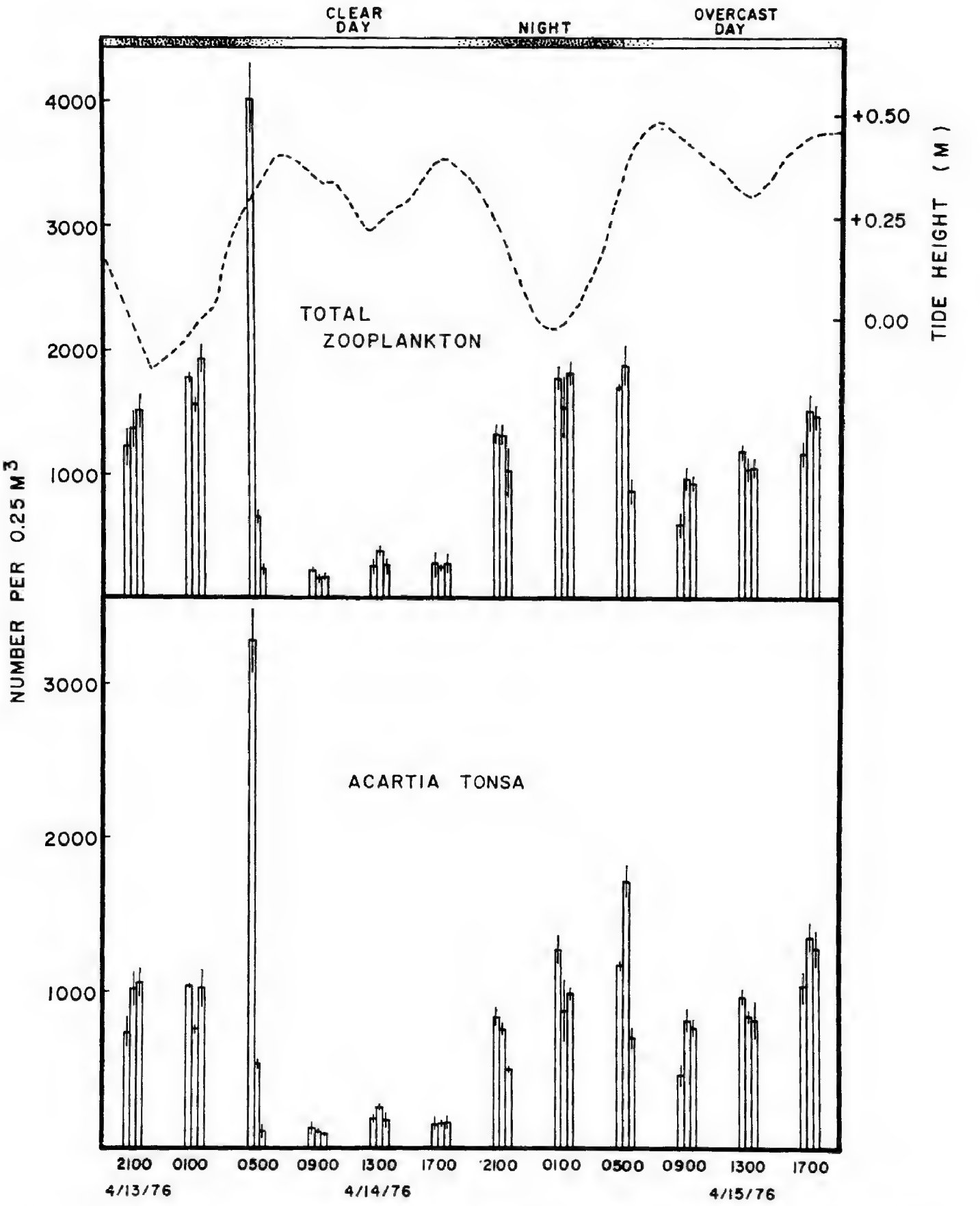

FIG. 2. Densities of total zooplankton and *Acartia tonsa*. Bars represent mean densities, calculated from three subsamples, for each tow taken over the 2-day sampling period. Within each sampling time, the means are arranged in the order in which the tows were taken. The vertical line through each bar indicates the 95% confidence interval calculated from the three subsamples. The dashed line represents the tidal level.

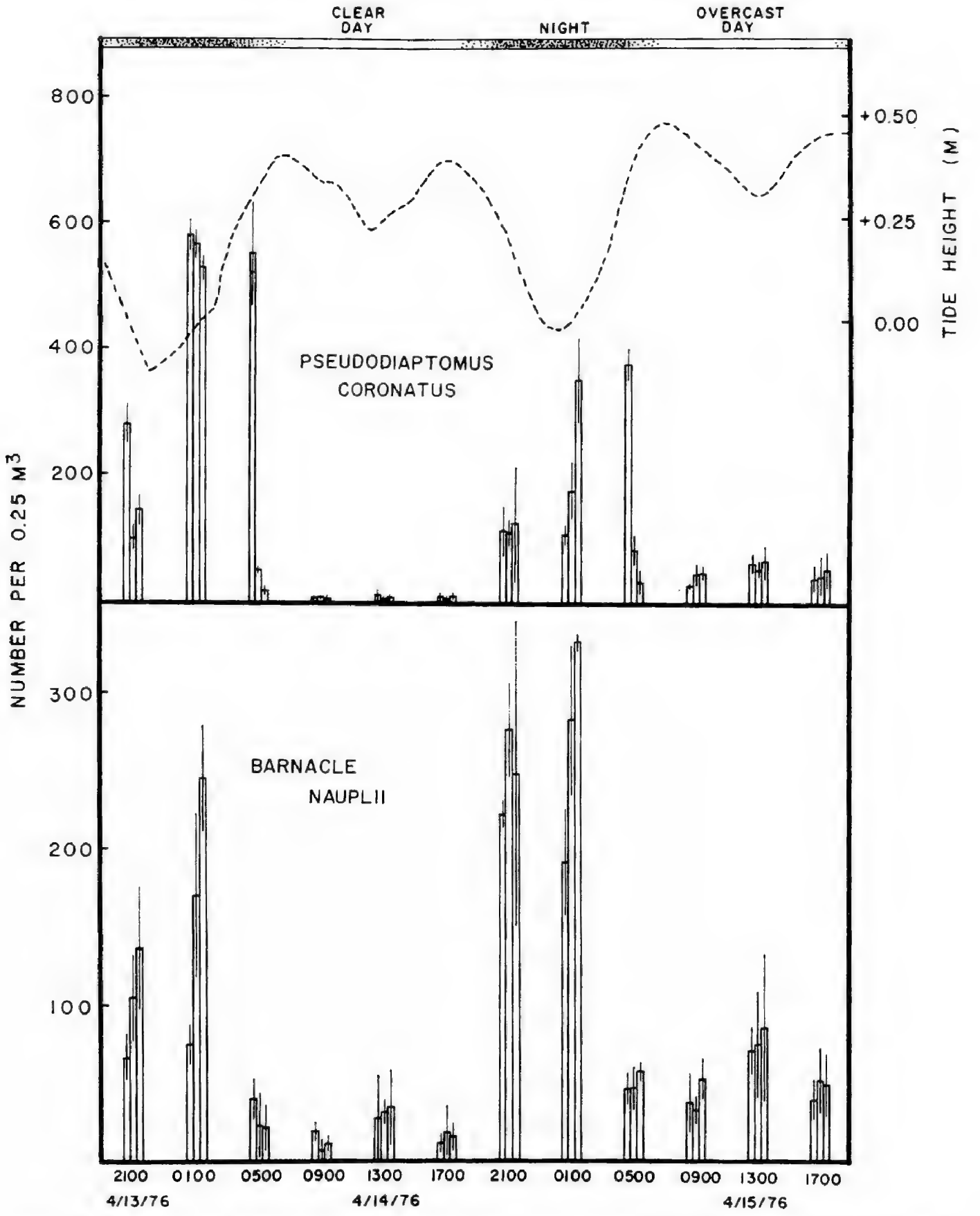

FIG. 3. Densities of *Pseudodiaptomus coronatus* and barnacle nauplii. Graphed as in Fig. 2.

(Table 1). Coefficients of variation calculated from the three replicate tows taken at each sampling time ranged from 3.4 to 126.5% for total zooplankton, 3.0 to 133.2% for *Acartia tonsa*, 4.7 to 147.0% for *Pseudodiaptomus coronatus*, and from 10.5 to 53.0% for barnacle nauplii (Table 4). The highest coefficients for *A. tonsa* and *P. coronatus* occurred near sunrise at 0500 hours on both days. Confidence intervals (95%) calculated from log transformed densities

TABLE 2

Duncan's multiple range test results comparing means from the 12 sampling times for the four categories of organisms examined. The replicate tow error term from the analysis of variance was used in this analysis. Sampling times are arranged in descending order on the basis of mean density. Sampling times connected by a line cannot be statistically distinguished at the 5% significance level.

Sampling sequence number	1	2	3	4	5	6	7	8	9	10	11	12
Sampling time	2100	0100	0500	0900	1300	1700	2100	0100	0500	0900	1300	1700
					4-14-76						4-15-76	

Total zooplankton

2 8 9 12 1 7 11 3 10 5 6 4

Acartia tonsa

12 9 8 1 2 11 7 10 3 5 6 4

Barnacle nauplii

8 7 2 1 11 9 12 10 5 3 6 4

Pseudodiaptomus cornatus

2 8 1 7 9 3 11 12 10 6 5 4

of total zooplankton for 10 of the sampling times (omitting the 0500 hour tows) ranged from 92–108% of the mean to 50–193% of the mean (n=3). The 95% confidence intervals were large for the 0500 hr tows on April 14 (1–1870% of the mean) and April 15 (33–269%).

Variability in zooplankton density estimates introduced in the laboratory was small in relation to the replicate tow variability. Laboratory error remained insignificant even when time period 3 (highest replicate tow variability) was eliminated and the analysis of variance was recalculated. The coefficients of variation for total zooplankton from the three subsamples taken from each sample ranged from 0.4% to 14.3% with a mean of 4.4% (SD= 3.0, n= 36). Since laboratory error could be attributed to subsampling or counting error, the organisms in six subsamples were counted twice. Subsampling error appeared to be approximately 3.5 times as important as counting error.

TABLE 3

Temperature, salinity, and turbidity measurements from surface water samples for the 12 sampling times. Surface wind speeds are also indicated.

Sampling time	Temperature (°C)	Salinity (ppt)	Turbidity (% trans.)	Wind speed (km/hr)
4-13-76				
2100	24.1	24.5	92	26
4-14-76				
0100	23.9	24.0	92	23
0500	23.0	24.0	92	21
0900	23.2	24.0	92	23
1300	24.4	24.0	91	24
1700	25.1	24.5	91	26
2100	24.1	24.5	93	26
4-15-76				
0100	24.0	25.0	94	27
0500	23.3	24.5	90	24
0900	23.4	24.5	88	26
1300	23.6	25.0	82	34
1700	23.5	25.0	81	37

DISCUSSION

The overall results indicated that relatively little variability in our density estimates could be attributed to subsampling and counting error. Similar conclusions have been made by Wiebe, Grice, and Hoagland (1973) and by Lee and McAlice (1979). Subsampling with the Hensen-Stempel pipet appears to be reliable for small (approximately 1 mm or less animals with the possible exception of high density organisms such as shelled molluscs. Since this subsampling method did not introduce any appreciable variability into our results, replicate subsampling of samples with a similar species composition is probably unnecessary.

Although the pooled variability from replicate tows (those taken at approximately the same time) was high in relation to laboratory error, it was relatively low compared to the variability among sampling times. Despite differences in sampling designs and methods of analysis, the replicate tow variability as indicated by coefficients of variation and 95% confidence intervals for 11 of the 12 sampling times (excluding time period 3) is comparable to other published data on estuarine sampling variability (Hopkins 1963, Carpenter, Anderson, and

TABLE 4

Coefficients of variation (%) for the 12 sampling times. Values were calculated from mean densities (untransformed data) for the three tows taken during each time period.

$$\text{C.V.} = \text{SD}(100)/\overline{\text{X}}$$

Sampling time	Total zooplankton	*Acartia tonsa*	Barnacle nauplii	*Pseudodiaptomus coronatus*
4-13-76				
2100	10.6	17.7	34.2	54.4
4-14-76				
0100	10.5	17.9	52.2	4.7
0500	126.5	133.2	37.7	147.0
0900	18.8	18.5	53.0	19.9
1300	14.6	21.1	10.5	42.6
1700	3.4	3.0	23.2	21.1
2100	13.7	25.0	10.9	5.8
4-15-76				
0100	8.4	19.3	26.7	60.4
0500	36.4	42.2	13.6	116.2
0900	24.9	27.4	26.4	31.1
1300	6.8	9.0	10.3	9.2
1700	13.6	13.8	13.6	18.2

Peck 1974, Sameoto 1975, Lee and McAlice 1979). Most of the variability among replicate samples in other studies has generally been attributed to the small scale patchy distribution of organisms, which also may have been important in our samples. The greatest variability among the 12 sets of three replicate tows in our study, however, occurred near sunrise at 0500 hours. The high variability in these samples could be explained by the downward movement of organisms out of the range of our net during the time needed to make the three tows.

Most of the variability among our 12 sampling times can be attributed to the diel vertical migration of organisms or to the movement of large patches of zooplankton past the sampling area due to tidal flow. Because tidal changes coincided with changes in daylight during our 2-day sampling period, these factors are confounded. Although the effect of tides on zooplankton sampling results has generally been regarded as important in estuaries (Hopkins 1963, Trinast 1975, Lee and McAlice 1979), tidal fluctuations in most of West Bay are small and are probably of little significance. Evidence from our study strongly suggests that changes in the vertical distribution of organisms were a major factor influencing the variability among sampling times. The high zooplankton densities observed during the night tows and the low densities during the day tows were consistent with the typical diel migratory pattern exhibited by many zooplanktonic organisms. *Acartia tonsa*, *Pseudodiaptomus coronatus*,

and barnacle nauplii made up approximately 90% of the organisms captured in this study, and densities of all three groups were highest during night tows. Other studies in the Galveston Bay System (McAden 1977), the coastal waters off Galveston (Allison 1967), and in other estuarine areas (Jacobs 1961, Youngbluth 1980) have indicated that *A. tonsa* undergoes typical diel migrations. Although evidence for typical migratory behavior in barnacle nauplii is conflicting, McAden (1977) concluded that these organisms also migrated towards the surface at night. The large day-night differences in the density of *P. coronatus* also support the importance of diel migrations in our samples. This species was rarely captured in our daytime tows. *Pseudodiaptomus* is known to be a strong vertical migrator (Grice 1953, Jacobs 1961, Pillai and Pillai 1973), and it has been suggested by Grice (1953) and Jacobs (1961) that copepodids and adults of *P. coronatus* may be demersal, in which case they occupy the water column during the night and become associated with a substrate during the day.

Zooplankton densities were also significantly higher during the daylight hours of April 15 compared to this same time period on April 14, although tidal heights were similar on both days. On April 14 the sky was clear and winds were relatively calm. On April 15, however, the sky was overcast and the wind increased vertical mixing in the water column as evidenced by the increase in turbidity. Both of these factors, an overcast sky and an increase in vertical mixing, would tend to prevent a strong migration away from the surface during the daylight hours of April 15. The extent of vertical mixing in the water column may be especially important in relation to the daytime catch of *P. coronatus*. Perry (1970) found in a Mississippi estuarine system, when sampling during the day, that most of her catch of *P. coronatus* was in shallow turbulent waters.

Although our sampling was limited to a 2-day period in the spring, the large fluctuations observed in zooplankton densities should be considered when interpreting other data obtained through similar sampling methods. Total zooplankton densities on both nights were similar, but they were approximately 6 times greater than daytime densities on April 14. Daytime densities on April 15 were 3 to 5 times greater than on April 14. This day-to-day variability may be especially important and apparent seasonal or spatial variations of these magnitudes could be attributed to short-term sampling variability.

To improve methods of estimating zooplankton densities in shallow estuaries, light and weather conditions should be considered. The vertical migratory behavior of the zooplankton apparently influences sampling results even in extremely shallow estuaries. To obtain comparable density estimates from net tows, an effort should be made to avoid sampling near sunrise or sunset. Day tows should not be compared to night tows, and sampling should be conducted under similar wind and sky conditions if possible. The most accurate method of estimating zooplankton densities will involve obtaining at least one oblique tow during the day and one during the night from each station. Night sampling in these estuarine systems is difficult however, and may not be practical. The use

of a pump to sample the entire water column during the day is another alternative. Pump sampling, however, is only adequate for the smaller zooplanktonic organisms and will underestimate densities of demersal zooplankton.

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CHARACTERISTICS OF PHYTOPLANKTON PRODUCTION OFF BARATARIA BAY IN AN AREA INFLUENCED BY THE MISSISSIPPI RIVER

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ABSTRACT

Phytoplankton particulate production was measured in coastal waters along a transect west of the Mississippi River delta using *in situ* and light-box techniques. Seasonal changes in light-box surface production (0.2–155.0 mg $C \cdot m^{-3} \cdot h^{-1}$), chlorophyll *a* (1–26 mg Chl $a \cdot m^{-3}$), *in situ* water column production (9.5–186.0 mg $C \cdot m^{-2} \cdot h^{-1}$), and assimilation number (0.15–42.0 mg C·mg Chl $a^{-1} \cdot h^{-1}$) were all correlated with riverflow. Seasonal changes in the riverflow volume altered the nutrient supply, water color, turbidity and salinity/temperature regimes. Changes in nutrient concentrations were indicative of nitrogen limitation. Annual particulate phytoplankton production was 290 g $C \cdot m^{-2}$.

INTRODUCTION

This paper presents information on phytoplankton production and nutrient concentration in the coastal waters off Barataria Bay near the Mississippi River delta. The largest river in the U.S. drains 41% of the country, passes through a well-developed industrial corridor, then annually debouches into these coastal waters (where 30% of the annual U.S. fish harvest is caught) over 3.4×10^9 kg carbon with a C:N ratio of 8:1 (Malcom and Durum 1976). The impact of Barataria Bay on these waters is not exactly known. Happ, Gosselink, and Day (1977) estimate that 260 g organic matter per m^2 of open water in the estuary is exported offshore annually. An outwelling of nutrients from estuary to nearshore has not yet been demonstrated for Barataria Bay, though it apparently occurs elsewhere (Kjerfve and McKellar 1980).

Murray (1976) provides a concise summary of the published information on the physical oceanography of this area. Longshore currents are predominantly westward, except during summer when they flow eastward. The surface Mississippi River plume usually curls northwestward toward Barataria Bay; the salinity of the bottom layer is at least $33^0/_{00}$. There is little published material on the biological oceanography, however; and synoptic sampling of the plankton community is rare. The works of Riley (1937), Thomas and Simmons (1960) and El-Sayed (1972) are good but limited to a few samples from a small area. Fucik (1974) studied phytoplankton production at two stations in deeper

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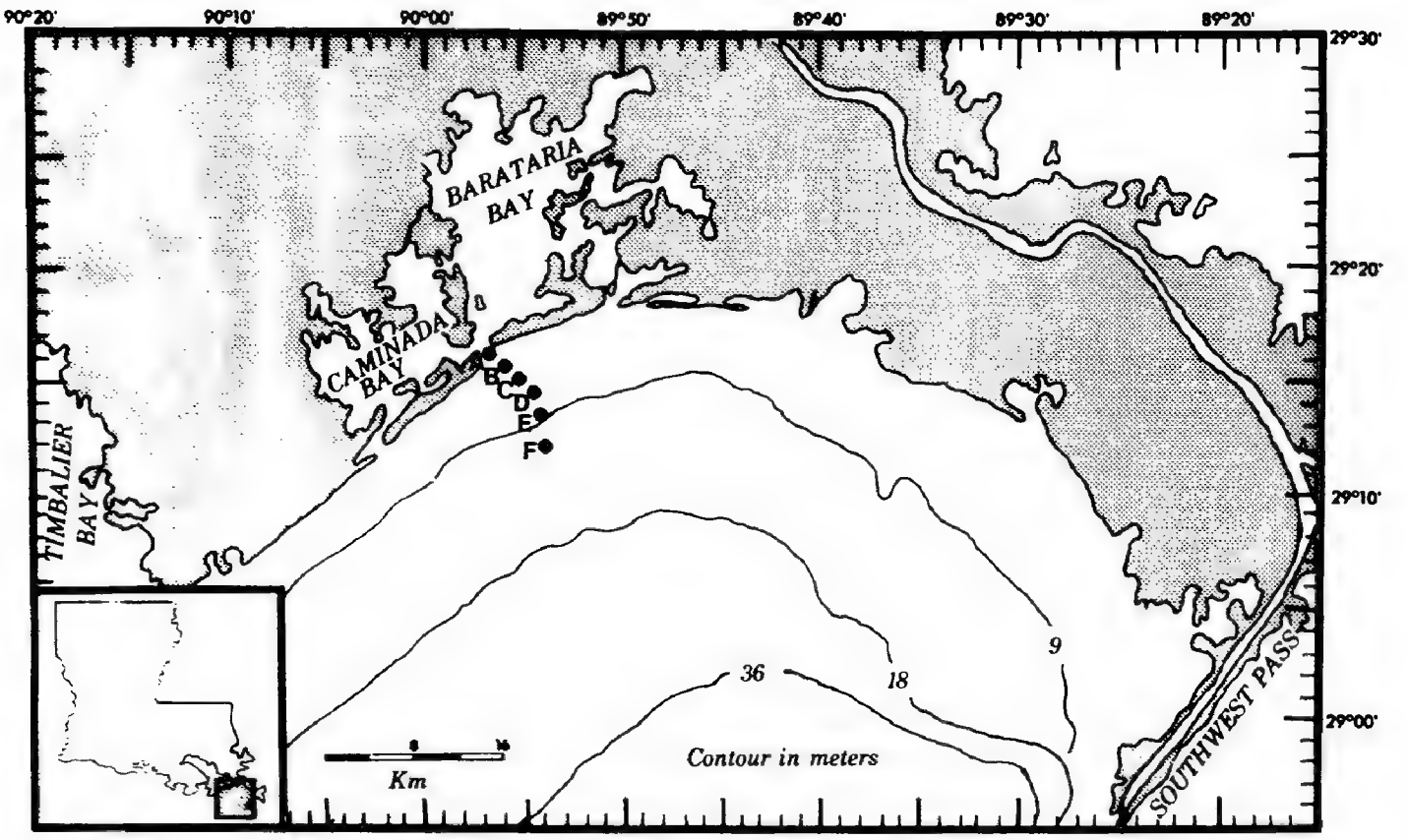

FIG. 1. The sampling area and stations.

water westward, off Timbalier Bay and much farther from our stations (Fig. 1).

The objectives of this contribution are to (1) present new data on the spatial and temporal variations in primary production and nutrient concentrations along a nearshore transect 40 km NW of the Mississippi delta, (2) compare chemical and biological characteristics of the differently colored water masses therein, and (3) suggest general relations between the plankton community and the physical oceanography of the area.

METHODS

From August 1974 to September 1975, we sampled three to eight days monthly at six stations (Fig. 1). Samples were collected along a transect from station F to the entrance of the Barataria Bay estuary. Experiments were conducted aboard the Freeport Sulfur Platform (station F). Water samples were collected at the surface at all stations and with depth at station F with a 1-l. Niskin bottle. Primary productivity (particulate carbon only) was measured using the C^{14} technique outlined in Strickland and Parsons (1968). We employed two sampling and incubation strategies to measure phytoplankton production rates. The purpose of the first approach was to measure the relative primary production rates of the surface water samples collected between 1100 and 1300 h along the transect shown in Fig. 1. Duplicate subsamples were put into 50 ml vials with one ml of C^{14} solution and incubated for two to four hours at *in situ* temperature in a light-box equipped with a panel of cool, fluorescent lights (4.1×10^3 $\mu w \cdot cm^{-2}$).

In situ primary production was simulated monthly with the second approach at station F. We placed duplicate subsamples of water collected between 1100 and 1300 h in 125 ml BOD bottles, inoculated them with one ml of C^{14} working solution, and then resuspended them at the depth from which the sample was taken for four to six hours. A minimum of five depths including surface and 1% light level were always taken. The stainless-steel, upside-down, T-

shaped rack holding the two light and two dark bottles was held steady by a wire anchored to the sea bottom. Fourteen complete *in situ* analyses were made.

Following incubations, the plankton filtered onto 0.45 μ cellulose membrane filters were acid-fumed for 10 minutes and subsequently dissolved in a toluene-dioxane fluor to measure isotopic activity by liquid scintillation (Wolfe and Schelske 1967; Iddings 1969; Pugh 1970). Isotope uptake was converted to hourly and daily rates following corrections for isotopic dilution, dark bottle uptake, incubation period, sample volume, and scintillation counting efficiency. Production per area was calculated using the vertically integrated results from the *in situ* incubations. The coefficient of variation for the error due to technique and for the error due to temporal and spatial variation was 9.4 percent (n = 5) and 26.4 percent (n = 5), respectively; this is similar to the results reported by Cassie (1962).

Chlorophyll *a* concentrations (minus phaeopigments) were determined spectrophotometrically (Strickland and Parsons 1968; Lorenzen 1967). Total dissolved inorganic carbon was estimated by adapting Menzel and Vaccaro's (1964) method for measuring organic carbon for use with an infrared gas analyzer. The Kjeldahl nitrogen, nitrate, and nitrite-nitrogen (NO_3 + NO_2–N), ammonium-nitrogen (NH_4–N), organic-nitrogen, total-nitrogen, orthophosphate, and total phosphorus concentrations of unfiltered samples were measured using Ho and Barrett's (1977) minor modifications of procedures described in Strickland and Parson's manual (1968). Individual numbers for primary production, nutrients and chlorophyll pigments for each sampling date and depth are available in Sklar (1976).

Three water color types, 'brown', 'green', and 'blue', are easily identified at the sample stations. We noted color character at each sampling; a students 't' test was used to compare different water mass characteristics. A secchi disk was employed to estimate turbidity and the 1% surface light depth.

RESULTS

The Mississippi River waterflow was 27% higher during 1975 than the 1940–1977 average. Maximum flow was in spring (March–May), 2×10^{12} m^3, whereas maximum rainfall occurred in summer (Fig. 2). Water temperatures

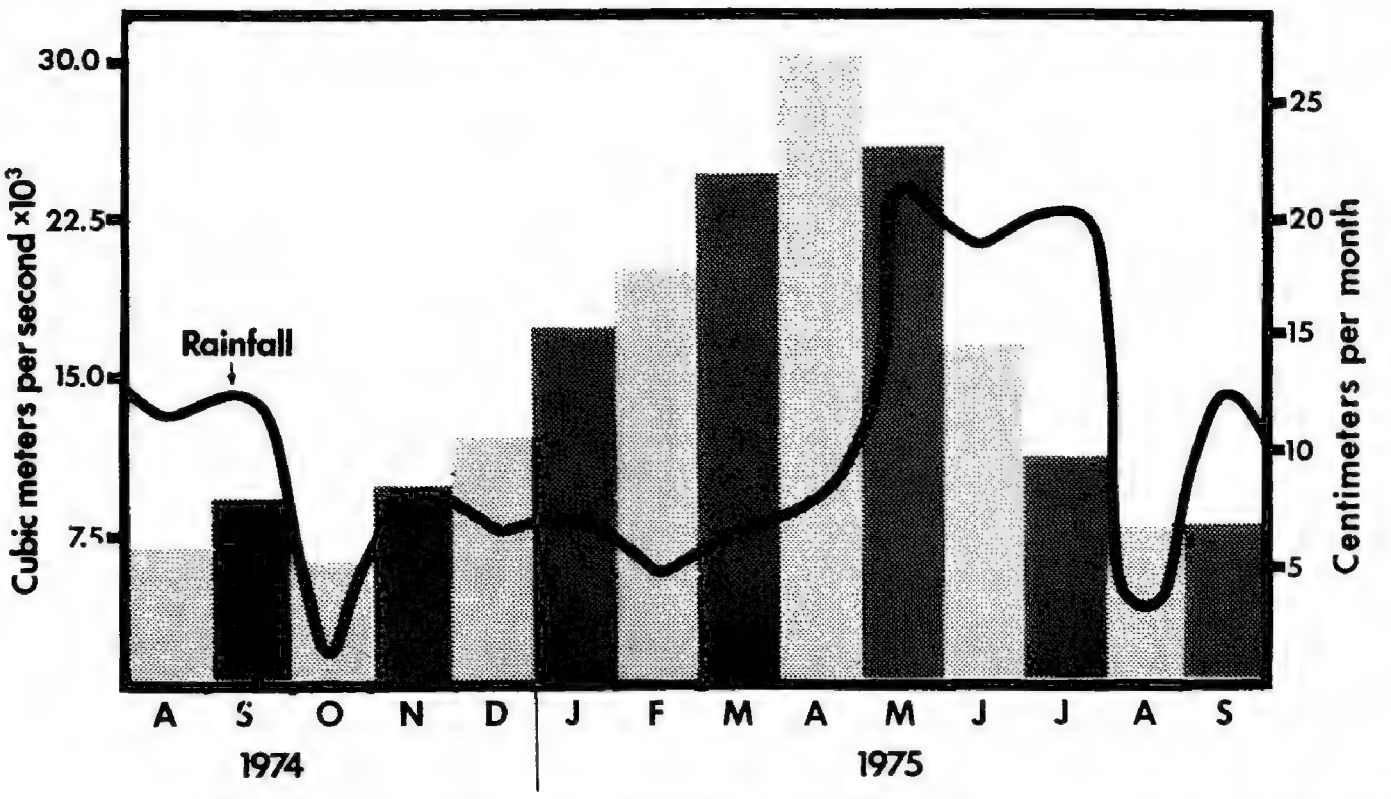

FIG. 2. The monthly discharge of the Mississippi River and local rainfall near the sampling area.

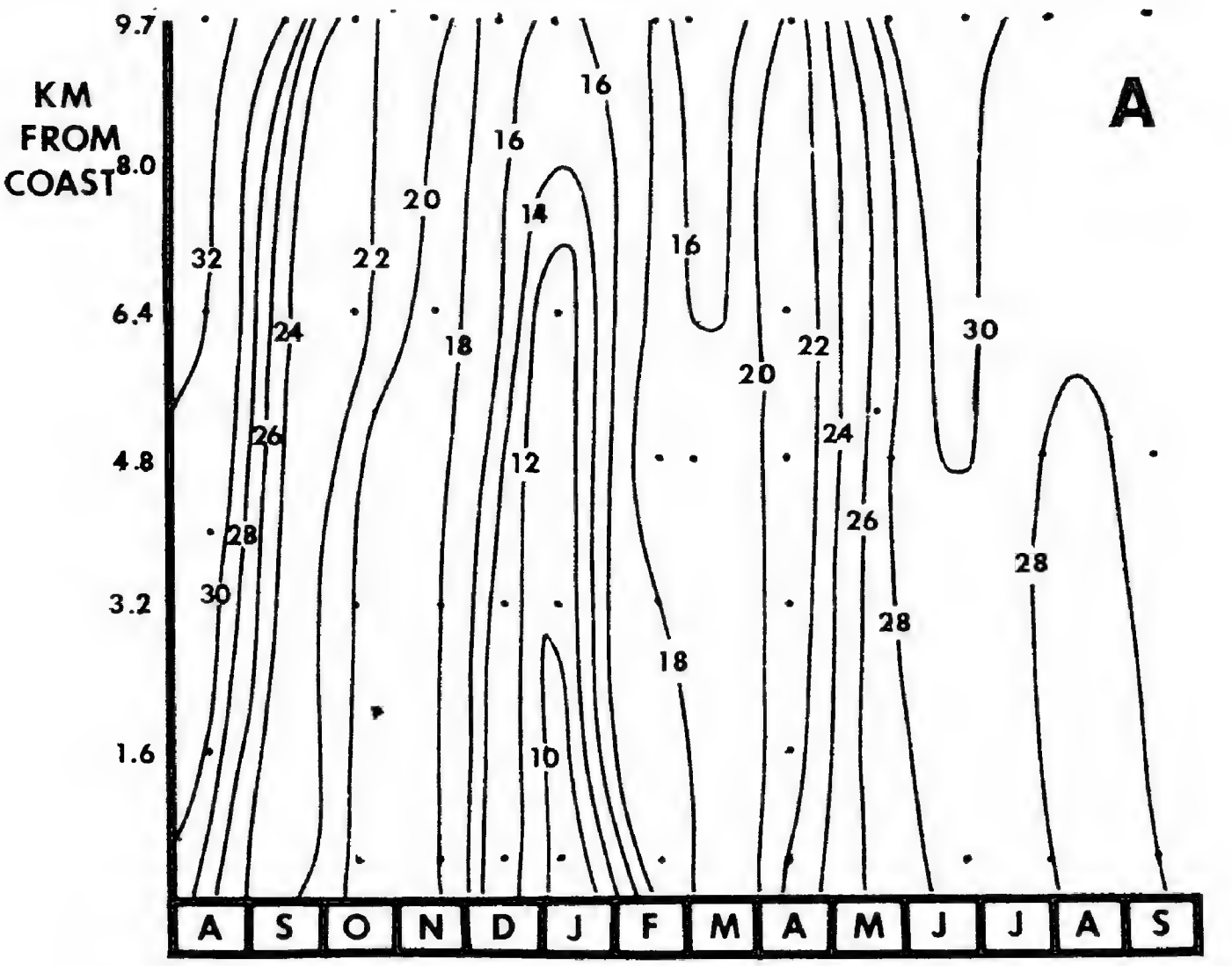

FIG. 3. Seasonal variations in temperature (A) and salinity (B) along the transect from station A to station F.

ranged from 10°C to 32°C (Fig. 3A). Offshore water were generally warmer in the winter and colder in the spring (during high river discharge) than nearshore waters. Salinity ranged from 10 ‰ to 30 ‰ with offshore waters generally more saline than inshore waters, except during high river discharge in springtime (Fig. 3B). These data are consistent with the observations of Wiseman *et al.* (in press) that in springtime the cooler river water moves from the river delta northwestward and toward station F, and thus strongly influences the seasonal salinity and temperature regimes across the sampling transect.

The month-to-month fluctuations of all measured chemical components in the photic zone were great (Fig. 4). Monthly averages of ammonium—nitrogen (NH_4—N) ranged from 0 to 221 $\mu g \cdot l^{-1}$, nitrate+nitrite—nitrogen (NO_2+NO_3—N) from 0 to 458 $\mu g \cdot l^{-1}$, total nitrogen (TN) from 85 to 1661 $\mu g \cdot l^{-1}$, orthophosphates (O—P) from 1 to 100 $\mu g \cdot l^{-1}$ and total phosphate (TP) from 13 to 139 $\mu g \cdot l^{-1}$. There were some noticeable trends. The NO_2+NO_3—N concentrations were inversely related to the NH_4—N concentrations while the O—P concentrations remained relatively constant. Generally, there was more NO_2+NO_3—N in the water than NH_4—N. Ho and Barrett's (1977) nutrient data for the region are similar to ours, though the range reported by them is less because they sampled quarterly.

The seasonal variation of nitrogen to phosphorus was high in the winter and low in the summer (Fig. 5). The mean atomic ratio of 104 samples for NH_4+NO_2+NO_3—N:O—P (NN:P) was 16.0, and for NO_2+NO_3—N:O—P (N:P) it was 11.4.

Photosynthesis rates, measured by utilization of the flourescent light box, are used here to compare rates in different areas at different times. Surface samples incubated in the light-box were compared to those incubated *in situ* for nine different times of the year. The coefficient of correlation (r) for those data was 0.60 ($P<0.05$). The regression slope of 0.5, however, indicates that the available light in the light-box was lower than *in situ.*

The light-box measurements of primary production are shown in Figures 6A and 6B. Generally, production in surface waters decreased with increased distance from the coast. February and March, however, were times when the opposite was observed. Figure 6B shows the monthly production estimates. Surface production measured in the light-box was generally greater in brown than the green water (175 g $C \cdot m^{-3} \cdot yr^{-1}$ vs. 102 g $C \cdot m^{-3} \cdot yr^{-1}$, respectively).

Twenty *in situ* surface primary production measurements were made throughout the year (except in March and April) at station F, a green water station. Surface production ranged from 0.82 to 165 mg $C \cdot m^{-3} \cdot hr^{-1}$. The mean of the monthly average *in situ* surface production ($n = 11$) was 365 mg $C \cdot m^{-3} \cdot d^{-1}$ (assuming a 12 h daylight period). Fourteen complete *in situ* vertical production measurements were also taken throughout the year at station F to estimate the total photic zone photosynthesis. Salinity and temperature profiles indicate that the photic zone was well mixed throughout the year; pigment concentrations, however, were highest at the surface for ten of fourteen samplings. The maximum recorded photic zone production for the year was 2.4 g $C \cdot m^{-2} \cdot$

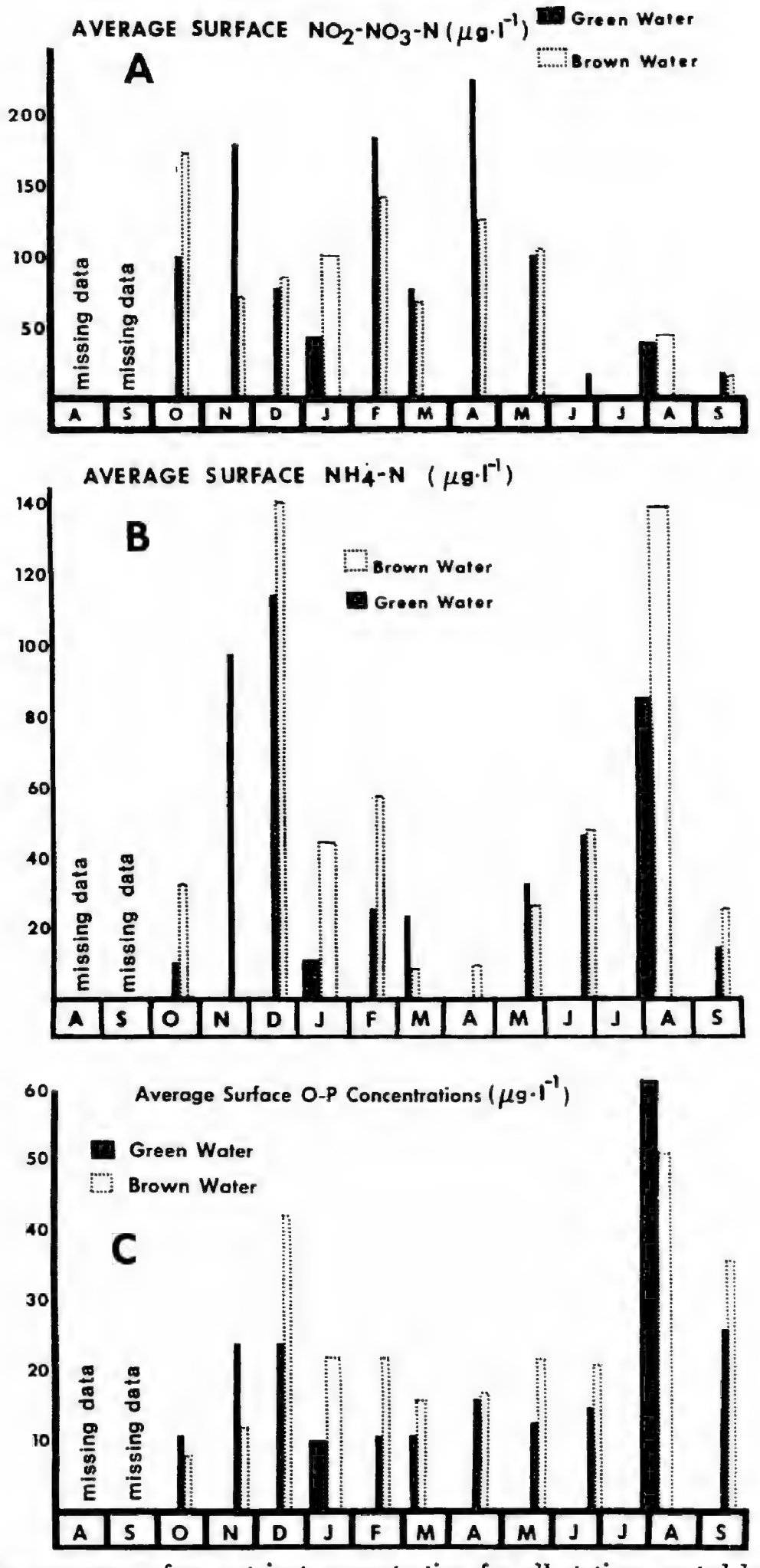

FIG. 4. The average surface nutrient concentration for all stations, sorted by water color. The bar width and position indicate the sampling period during the month. (A) Nitrate + nitrite nitrogen; (B) Ammonia nitrogen; (C) Orthophosphate.

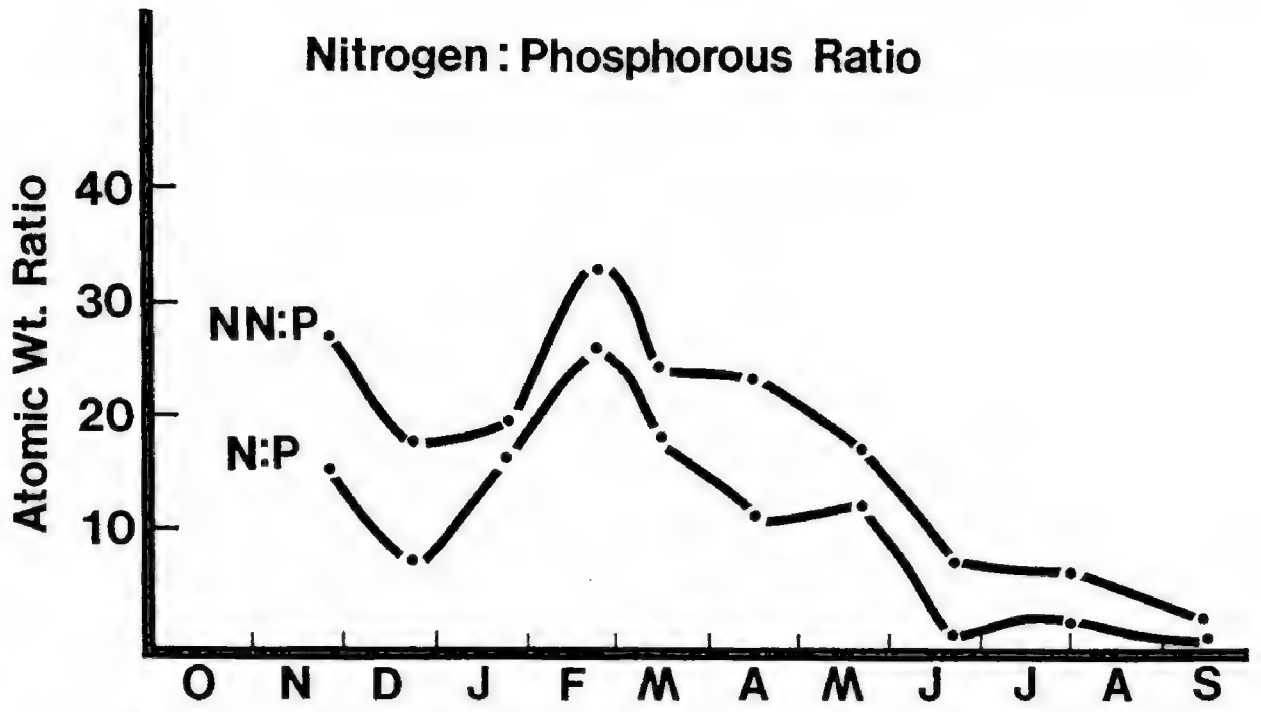

FIG. 5. The seasonal variation of available nitrogen to phosphorus, by atomic weight. The line labelled NN:P is the ratio of NH-4 + NO-2 + NO-3 N to O-P ($\bar{x} = 16.0$, standard error = 6.1). The line labelled N:P is the ratio of NO-2 + NO-3 — N to O-P ($\bar{x} = 11.4$, standard error = 5.9).

d^{-1} in May; the minimum recorded was 0.1 m $C \cdot m^{-2} \cdot d^{-1}$, in November. The mean of the monthly average photic zone production, interpolated for 3 missing months, with an average day length of 12 h, was 290 ± 247 g $C \cdot m^{-2} \cdot yr^{-1}$ (u ± 1 S.D.).

The seasonal pattern of surface production measured in the light box and *in situ* coincided with seasonal changes in river discharge (Fig. 2). Areal production measured *in situ* exhibited a pattern similar to surface production (Fig. 6) except for a second peak in late summer. The latter phenomenon we attribute to increased light penetration as a result of decreased suspended sediments in the water column (see Discussion).

High surface chlorophyll *a* concentrations between the shore and station F were recorded during spring and early summer when solar insolation and primary productivity were at a peak (Fig. 7). Measurements ranged from 0.75 to 26.6 mg Chl$a \cdot m^{-3}$ and averaged 6.2 ± 0.73 mg Chl$a \cdot m^{-3}$. Chlorophyll *a* concentration in the photic zone averaged 17.9 ± 5.2 mg Chl $a \cdot m^{-2}$.

The production per unit chlorophyll, or assimilation number, ranged from 0.15 to 42.5 mg C·mg Chl$a^{-1} \cdot h^{-1}$ and averaged 6.5 ± 0.7 mg C·mg Chl$a^{-1} \cdot h^{-1}$. The assimilation number was highest during January and March (Fig. 8).

Two water masses of brown and green color were easily distinguishable. A blue water mass, farther offshore and adjacent to the intermediate green water, was observed only once during sampling and was excluded from this analysis. T-tests were used to determine if there was a significant difference between the means of variables measured in both brown and green waters (Table 1). Surface productivity ranged from 0.15 to 126.2 mg $C \cdot m^{-3} \cdot h^{-1}$ in green waters and from 0.82 to 170 mg $C \cdot m^{-3} \cdot h^{-1}$ in brown waters. The mean daily surface production for brown waters was almost twice that of green waters (0.48 ± 0.1 g $C \cdot m^{-3}$

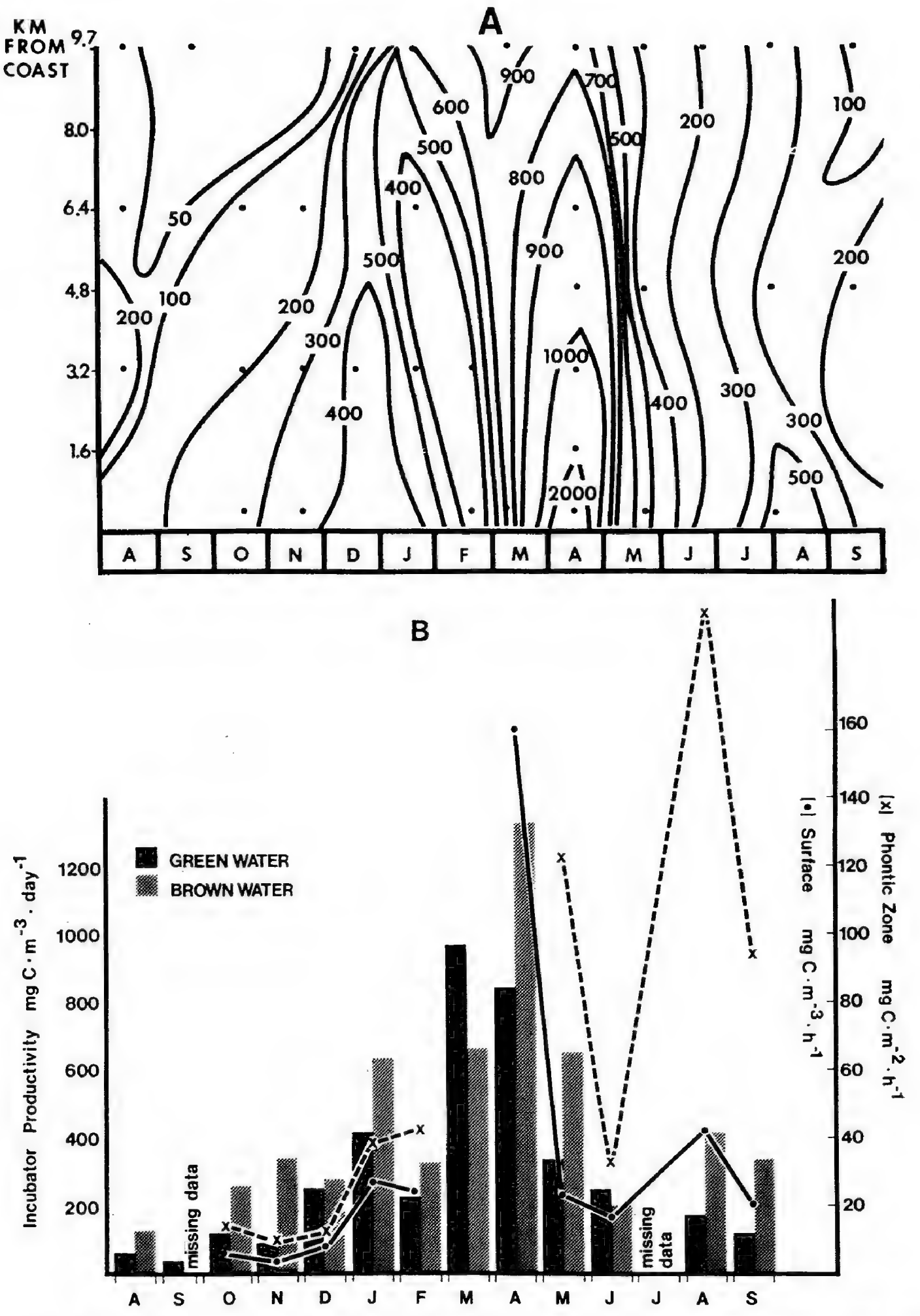

FIG. 6. (A) Phytoplankton production (mg $C \cdot m^{-3} \cdot day^{-1}$) in the surface waters along the transect from station A to station F. Samples were incubated in a fluorescent light bath. (B) Monthly averages of phytoplankton production in different water masses at station F. Samples were incubated in a fluorescent light bath (bars) and *in situ* (circles and x's).

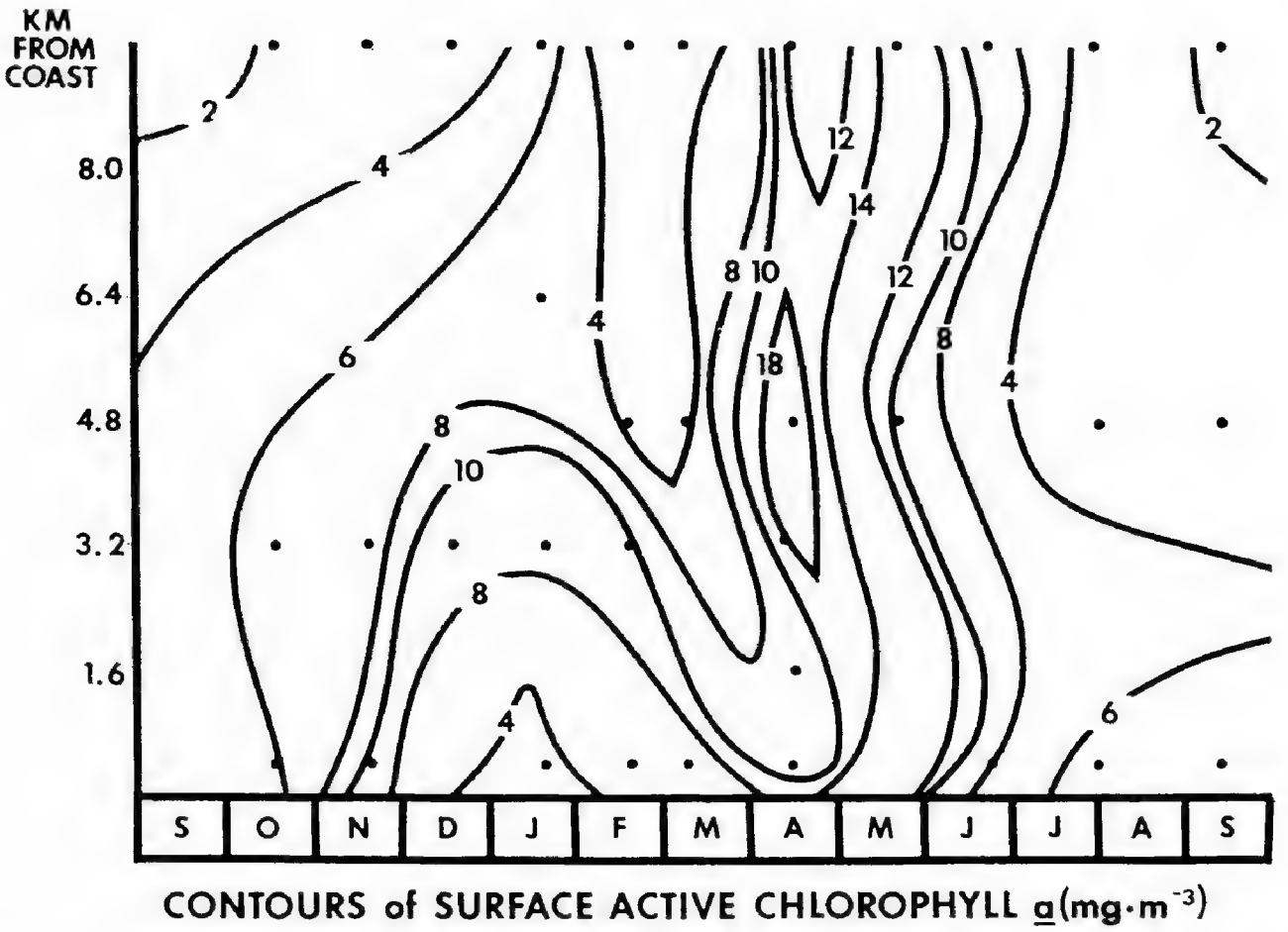

FIG. 7. Chlorophyll *a* concentrations in surface waters along a transect from station A to station F.

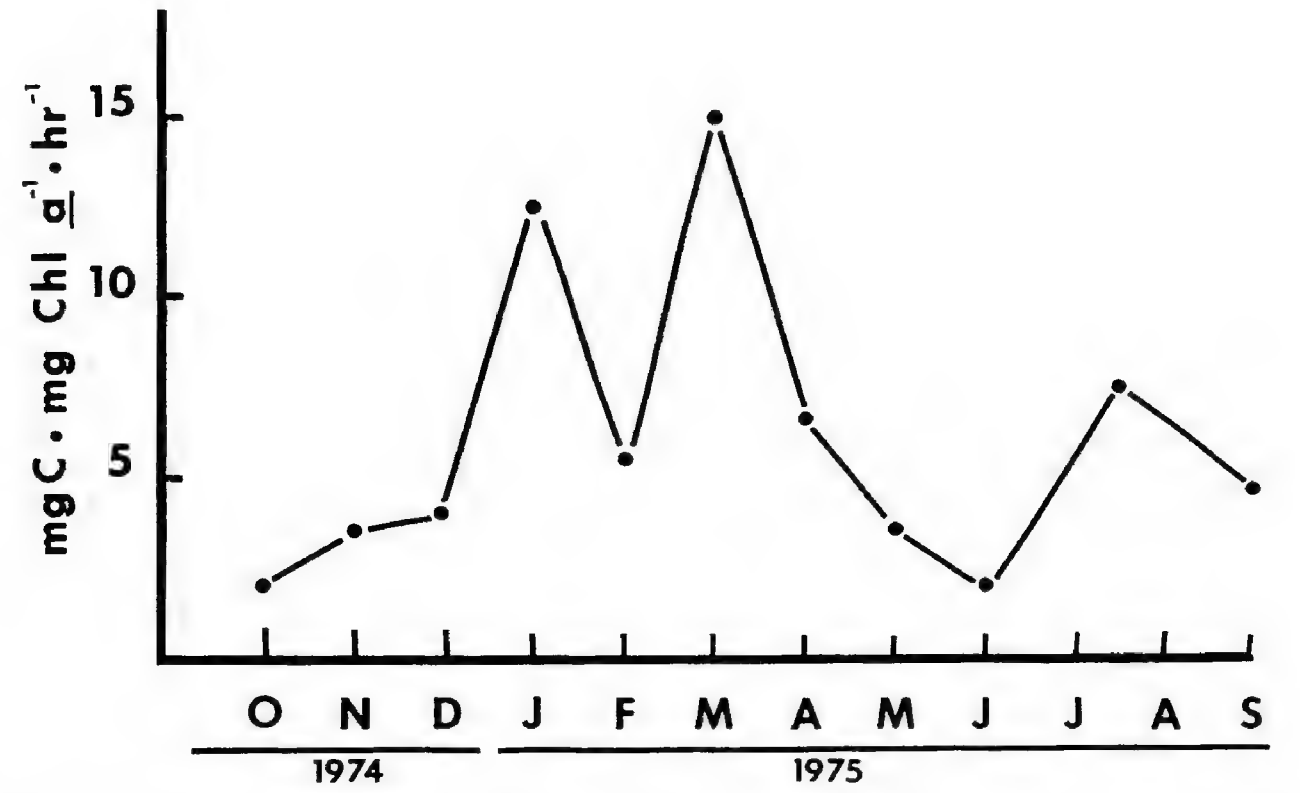

FIG. 8. The average monthly assimilation rate (mg C·mg chla^{-1}·h^{-1}) at all stations for surface samples incubated in the light box.

TABLE 1

A comparison of chemical and biological characteristics in brown and green-colored surface waters within the study area.

Variable	BROWN WATER (n)	Mean	Min.	Max.	GREEN WATER (n)	Mean	Min.	Max.	Probability of equal means P> t
Secchi depth (m)	(49)	1.0	.15	5	(65)	2.3	.5	6	**
Salinity (°/$_{oo}$)	(48)	19.5	5	30	(64)	24.5	7	34	**
Temperature (°C)	(49)	20.2	10	31	(66)	22.5	11	32	*
Total phosphorus ($\mu g \cdot l^{-1}$)	(38)	67	26	139	(54)	54	13	123	**
Orthophosphorus ($\mu g \cdot l^{-1}$)	(38)	26.9	2	75.9	(54)	22.5	1	100	n.s.
Total nitrogen ($\mu g \cdot l^{-1}$)	(37)	696	85	1661	(55)	517	139	1017	**
NH_4^+-N ($\mu g \cdot l^{-1}$)	(38)	56.2	0	201	(55)	48.5	0	173	n.s.
NO_2+NO_3-N ($\mu g \cdot l^{-1}$)	(37)	82.7	0	348	(55)	70.7	0	272	n.s.
Inorganic carbon ($mg \cdot l^{-1}$)	(49)	23.1	10.1	35	(66)	23.7	10.4	33.4	n.s.
Chl. *a* ($mg \cdot m^{-3}$)	(48)	7.9	.75	26.6	(62)	4.5	.75	15	**
Productivity ($g\ C \cdot m^{-3} \cdot d^{-1}$)	(43)	.48	.06	1.8	(49)	.28	.003	1.5	**
Dark uptake of carbon ($mg\ C \cdot m^{-3} \cdot d^{-1}$)	(43)	23.9	.47	370.8	(49)	10.6	.32	32.1	n.s.

*Significant difference at the 5% level.

**Significant difference at the 1% level.

n.s. No statistically significant differences.

and 0.28 ± 0.08 g C·m^{-3}, respectively). The Secchi disk depth in brown water was one-half that in the green water ($P<0.001$). Although the inorganic nutrient concentrations are not statistically different in both water masses, there were significant differences within certain sampling periods. For example, the NO_2+NO_3—N concentration was greater in green waters during April and greater in brown waters in January (Fig. 4). The brown water was slightly less saline than green water ($P<0.5$).

DISCUSSION

The spatial and temporal variations in biological, chemical, and physical parameters offshore of Barataria Bay present a very complex picture of coastal

processes. The river was the one consistent force influencing all parameters. Primary productivity, chlorophyll *a* concentrations, and assimilation number all peaked in the spring when riverflow was reaching a maximum; they were lowest when riverflow was at a minimum. Salinity decreased with increased distance from the coast when riverflow was high. Inorganic nitrate and nitrite nitrogen fluctuated in a similar manner, as did the nitrogen/phosphate ratio. The dilution of nutrient-rich, but turbid, river water by coastal waters appears to strongly influence the plankton community metabolism. It is useful, therefore, to discuss phytoplankton production as it is related to salinity and to include the data from Fucik (1974) and Thomas and Simmons (1960) (Fig. 9). Primary production in the surface waters at the delta mouth is quite low but increases rapidly as river water is diluted up to 10–20 percent. At each study area, the relationship of salinity to the assimilation number or surface primary production is of a similar pattern (Fig. 9, top and middle row). There is a peak at about 20–25 ‰. The production per unit area tends to follow the same pattern but is less clearly defined. Changes from east to west appear to produce a gradient of first increasing and then decreasing phytoplankton productivity. This zone of high production will change seasonally in response to hydrographic factors. General synoptic or quasi-synoptic surveys are therefore recommended in future studies of the area.

The N:P atomic ratio was usually much less than 15 and lower than 10 during summer, which thus indicates a potential for nitrogen limitation of phytoplankton production (Ryther and Dunstan 1972). Light is clearly an important limiting factor in the fresher and turbid waters, especially in the river plume. Surface production is probably light-limited near the river mouth and reaches some optimum balance between production per unit biomass and nutrient limitation near the 20 ‰ mixing zone. With further mixing and subsequent dilution, the water becomes clearer, but also relatively deficient in some essential nutrient(s). We suspect nitrogen to be a primary limiting nutrient; direct experimental evidence is not available yet. Other elements are also being diluted simultaneously with nitrogen. Thus, across the plume, offshore of both Barataria and Timbalier bays, the relationship between production·m^{-3} and salinity is the same. Decreases in surface production rates are compensated for by an increased amount of light but not biomass (Table 2). Thus, the assimilation number per m^3 at the surface (top, Fig. 9) is essentially the same at any given salinity value at all sites. Production per m^2, however, increases with an increased euphotic zine in a westward direction. A comparison of green and brown water (Table 1) supports these conclusions. The more turbid and slightly fresher brown water has an assimilation ratio similar to that of green, but higher nutrient concentrations and surface production. Production per m^2 is approximately equal in both water types, because a lower amount of chlorophyll *a* is compensated for by an increased euphotic zone.

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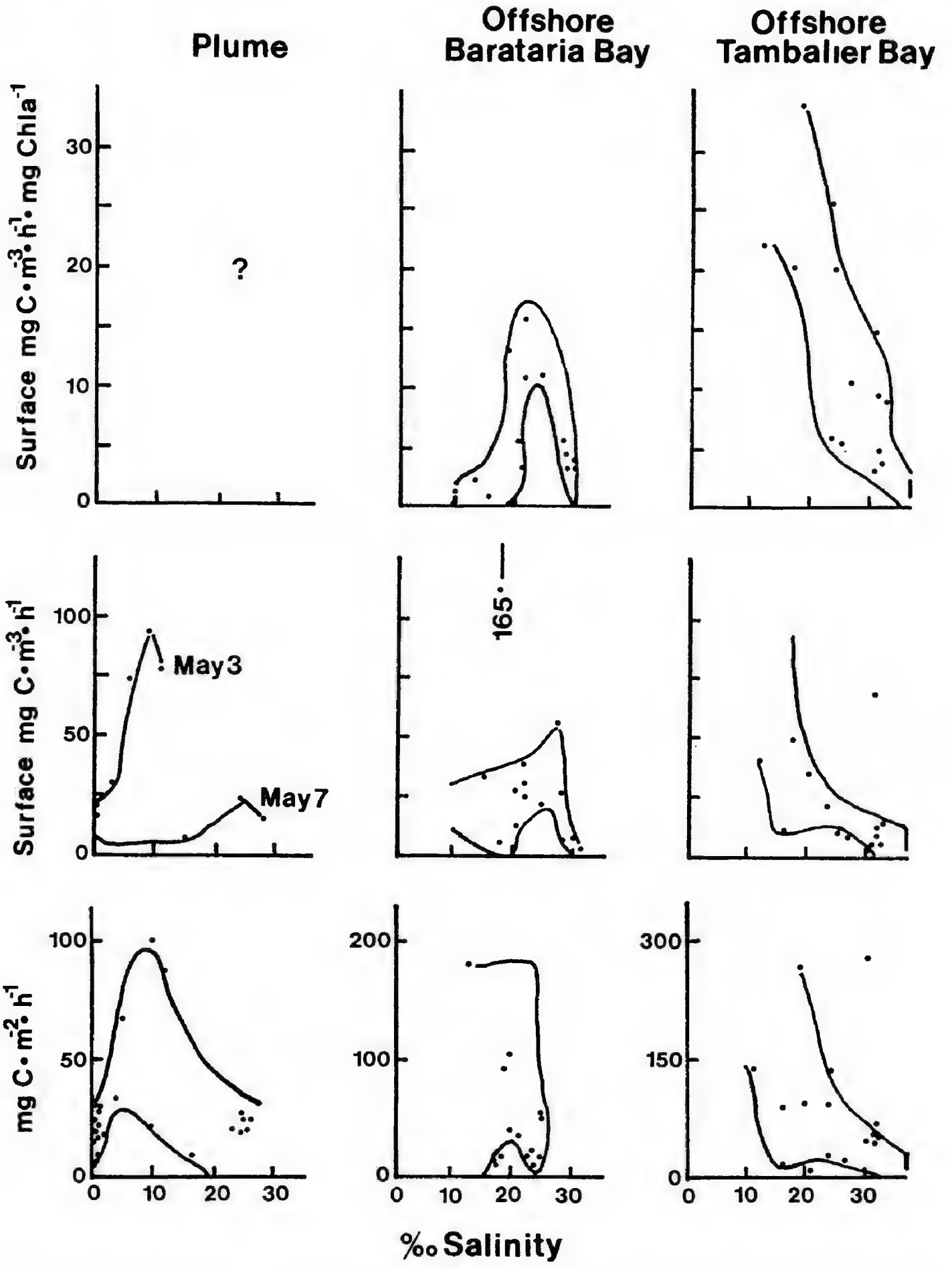

FIG. 9. Phytoplankton production in the Mississippi River plume (from Thomas and Simmons 1960), offshore near Barataria Bay (this study) and offshore near Timbalier Bay (from Fucik 1974) vs salinity. Monthly averages are depicted unless indicated otherwise. Dots are data points; the hand-drawn line is meant to outline the major trends. Note the scale change of each column for the y-axis on the bottom row. The station locations are arranged east to west, left to right across the page.

TABLE 2

Comparison of the monthly average conditions *in situ* at three sites near the Mississippi River Delta Bight.

	Plume[1]	Near Barataria Bay[2]	Near Timbalier Bay[3]
Secchi disk depth (m)	<2.0	1.0 'brown' water 2.3 'green' water	>10
Euphotic assimilation number (mg C·mg Chla^{-1}·hr^{-1})	---	4	11
Areal phytoplankton production (mg C·m^{-2}·hr^{-1})	1.0 - 5.8	66	91 - 101
Surface phytoplankton production (mg C·m^{-3}·hr^{-1})	0.21 - 1.0	38.4	26.0 - 27.0

[1]From Thomas and Simmons, 1960.

[2]This study, station F.

[3]Fucik, 1974; experimental and control sites.

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OIL SPILL EFFECTS ON SMOOTH CORDGRASS IN GALVESTON BAY, TEXAS

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Key Words: Oil spill, smooth cordgrass, Texas, Galveston.

ABSTRACT

Observations of the effects of number 6 fuel oil spilled into coastal waters and washed into *Spartina alterniflora* marshes were made near Galveston, Texas. Aboveground biomass of some fringing marshes was completely removed in November as part of a clean up operation. However, regrowth the following spring occurred with no noticeable effects on the plants. Oil also entered a larger marsh area, partly covering some plants and completely covering others. The oil killed the aboveground portion of a plant only when oil covered most of the plant. Plants, regardless of the extent of oil coverage, produced new growth in the following spring that appeared to be similar to other *Spartina alterniflora* communities of the area.

INTRODUCTION

The collision of an oil barge and tugboat on October 31, 1977 dumped 42,000 gallons of number 6 fuel oil into Houston ship channel waters adjacent to the tip of Bolivar Peninsula in Texas (Fig. 1). Much of the oil washed onto Bolivar Peninsula beaches and small fringing marshes of *Spartina alterniflora* adjacent to the ship channel. The plants were completely covered by oil. Oil also was carried towards the Gulf by tidal currents within the Houston ship channel, along the north jetty, through an existing boat cut, and was washed into several hectares of *Spartina alterniflora* marsh located east of the north jetty. Because many of the synthetic detergents and emulsifiers that are currently in use may cause the production of toxic byproducts (Manahan 1975, Cowell 1969) only 3M, a synthetic absorbent agent, was used by workmen in removal of oil in the spill studied.

A number of factors are important in determining the influences of oil on the biota of salt marshes. The type of oil determines the various types of hydrocarbons, aromatic fractions, napthlene components, etc., that vegetation and organisms may be exposed to. Aromatic fractions are the most water soluble (Gillman 1977); thus, they may penetrate into plants through stomata. Toxic

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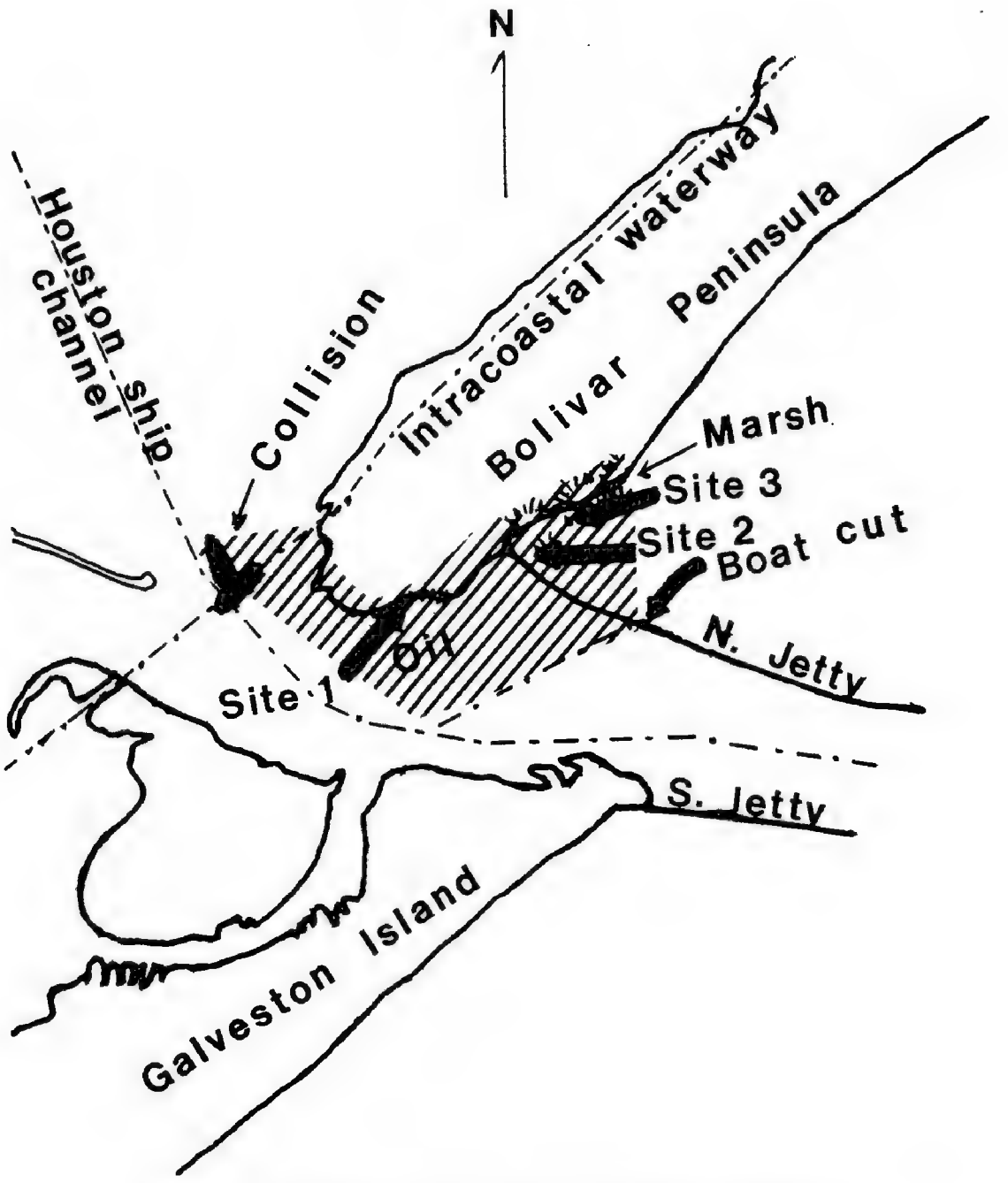

FIG. 1. Location of oil spill near Galveston, Texas.

oils can penetrate directly from the point of contact (Boesch, Hershner, and Milgram 1974, pp. 21–22). Hershner and Moore (1977) state that No. 6 fuel oil is relatively nontoxic as compared to a lighter fuel oil or a crude oil.

Plants are sensitive to oil because of (a) the high affinity between plant cuticle and oil hydrocarbons, (b) the obstruction of leaf pores, which restricts gas exchange between the plant and atmosphere, (c) the reduction of light available for photosynthesis, and (d) the toxicity of some oil constituents to metabolic processes. Plants with large underground vegetative stems survive oiling better than those plants without them, since new growth can occur from the stems after shoots and leaves have been destroyed (Baker 1970).

The amount of weathering by wind and wave energies and biodegradation, which oil is exposed to prior to reaching salt marsh vegetation, can be important. Constant agitation caused by wind and waves act to break up the oil into particulate oil droplets. Due to the proximity of the oil spill to the shore, little weathering of the oil occurred prior to adhesion to plants.

Response of plants to weathered and unweathered oil and to amounts of oil have been recorded by various authors. *Spartina alterniflora* has been shown to be unaffected by Arabian crude oil sprayed on the 7.5 cm bottom portion of stems (Crow 1974). However, plants clipped prior to sprayings showed noticeable regeneration with sprayings of unweathered and 2-day weathered crude oil. Slight recovery occurred from treatments with 7-day weathered crude oil. When leaves of *Spartina townsendii* in England were covered by oil films from an oil spill, death of leaves occurred in 204 days, but new plant shoots were noted within 3 weeks unless large quantities of oil had soaked into the plant rhizosphere (Cowell 1969). Although Mackin (1950) stated that *Spartina alterniflora* and several other species were especially sensitive to Louisiana crude oil, the levels of application actually determined whether no damage occurred, initial damage occurred, or plants recovered after one year. Greenhouse and field studies of DeLaune, Patrick and Buresh (1979) indicated that *Spartina alterniflora* can tolerate a large amount of Louisiana crude oil without a short-term decrease in aboveground biomass. The findings of DeLaune *et al.* agree with those of Hershner and Moore (1977), who monitored the regrowth of *Spartina alterniflora* after the removal of the oiled shoots after a No. 6 oil spill on a saltmarsh in Chesapeake Bay. Hershner and Moore hypothesized that the low toxicity of oil, the time of year the spill occurred (February), and the comparatively high energy environment of the shoreline were key factors in minimizing the effects of oil. Cutting and quick removal of oil-soaked *Spartina alterniflora* apparently allows good regrowth where tidal flushing and wave energies are low (Mattson, Vallario, Smith, Anisfield, and Potera 1977).

Factors reported as influencing the effects of oil on vegetation are salinity, species and age of plants (Baker 1970), physiography of marsh, soil type and weather conditions which determine wave and current energies (Burk 1977). Owens (1978) reported that rate of penetration of oil into sediments normally increases with decreasing oil viscosity. Chronic pollution from summer reoiling by Bunker C oil trapped on plants and shoreline may cause death of marsh plants and intertidal biota (Thomas 1973). However, oil spill effects may be acute with no long-term effects (Cowell 1971).

The present study was undertaken to document the effects of oil spill on *Spartina alterniflora*, the only plant species affected. Unfortunately, the unforeseen occurrence of the oil spill did not allow the monitoring of some factors such as wave and current energies, amount of oil dispersion, and by-products, that could determine detrimental effects of the oil spill on vegetation. Effects of the oil and plant removal by workmen on the vegetation were documented.

METHODS

Observations were made immediately after clean up operations and the following year in the marsh fringing the Galveston channel (Site 1). In this area workmen had completely removed the standing *Spartina alterniflora* as they raked and shoveled the oil. Therefore, no biomass samples were taken at the time of the oil spill.

One area (Site 2) of the north jetty marsh affected by the oil was at a slightly lower eleva-

tion than the other 2 sites and the plants were coated with oil to a slightly higher elevational level than the other 2 sites. In this area plants were being sampled in an ongoing study at approximately monthly intervals from July 1977 through May 1978. Growth data from these plants were used to determine effects of the oil. Live and dead stem density and stem height were measured, and standing biomass was harvested at ground level within five randomly located 0.25 m^2 quadrats along transects in the area at monthly intervals. The harvested aboveground material was placed in plastic bags and transported to a laboratory at Texas A&M University at Galveston where it was separated into live and dead material, then dried and weighed. After removal of aboveground vegetation, belowground biomass was sampled by driving a 15.2-cm diameter and 30-cm long section of sharpened polyvinylchloride (PVC) pipe into the ground at the center of each quadrat. The PVC core sample was excavated and its contents placed in a plastic bag for transportation to a Texas A&M University laboratory. Belowground plant parts were separated from soil by washing on a 1.0-mm mesh screen. Belowground plant parts were separated into live and dead components. Color and turgidity were the criteria used to differentiate between live and dead roots and rhizomes (Valiela, Teal and Persson 1976). Plant parts were oven dried to a constant weight. All data are reported on a m^2 basis.

Observations of oil covered *Spartina alterniflora* were made in a slightly higher section (Site 3) of the marsh east of the north jetty on November 2, 1977 shortly after the oil spill occurred. Vegetation biomass samples in three 0.5 m^2 quadrats were clipped approximately 2.5 cm above ground in 4 replicate areas of this marsh site. The samples were dried and then weighed. Photographs also were taken of the areas. Qualitative observations were made of the regrowth in quadrats and of the oil covered vegetation at 2-week intervals through December 15. Qualitative visual observations were made the following spring and summer in these four areas of Site 3.

RESULTS

Channel Fringing Marshes (site 1)

Spartina alterniflora plants in the marsh fringing the Houston ship channel were completely covered by oil the day after the oil spill. However, the oil in the water broke into small particles and dispersed within 3 to 4 days, probably due to the strong northerly winds occurring at the time. Coast Guard spokesmen estimated that 25,000 gallons of oil had been cleaned off beaches after 5 days of work (Galveston Daily News, November 4, 1977). Workers completely removed the aboveground portions of the marsh plants along the ship channel within 3 weeks of the oil spill as they raked and shoveled the oil and 3M cleaning agent from the shoreline. Since the area normally receives heavy use by fishermen, further substrate compaction by workers was probably not significant in causing any additional damage. However, no measurements were made of compaction.

No regrowth of plants was observed during the winter. *Spartina alterniflora* shoots initiated growth from surviving roots the following spring and produced a stand of grass similar in height and appearance to that which had existed prior to the oil spill. Production of seeds in August and September occurred as normal. The oil in the marsh and removal of aboveground biomass portions of the plants did not appear by qualitative observations to have detrimental effects on the plants.

TABLE 1

Plant measurements for site 2 by months

Measurements	Sample Dates 1977 25 Jul	1977 25 Sep	1977 2 Nov	1978 7 Jan	1978 21 Mar	1978 29 May
Culm height, cm	136.2	135.6	137.2	77.9	87.8	116.6
Live aboveground biomass, g/m^2	1455.8	743.7	605.9	116.2	202.5	653.9
Dead aboveground biomass, g/m^2	699.4	811.0	605.1	872.2	700.0	776.2
Total aboveground biomass, g/m^2	2155.2	1554.7	1211.0	988.4	902.5	1430.1
Belowground biomass, g/m^2	1377.5	1901.4	1697.7	1326.6	1309.0	1158.3
Live culm density, no/m^2	224.0	349.6	290.4	166.4	308.8	249.6
Dead culm density, no/m^2	39.2	141.6	136.0	204.8	346.4	288.0

North Jetty Marsh (site 2)

Biomass, height, and density measurements were available on the plants at this site prior to the oil spill because of an ongoing study. In general, growth of plants from July 1977 through May 1978 indicated no adverse effect of the oil on *Spartina alterniflora* (Table 1). Culm height had increased from a January low of 77.9 cm to 116.6 cm by 29 May 1978. Live aboveground biomass increased from a winter low of 116.2 g/m^2 to 653.9 g/m^2 in May, 1978, which was larger than that of 2 November, 1977 (605.9 g/m^2). Dead aboveground biomass was variable with no consistent pattern; maximum biomass occurred in January. Total aboveground biomass decreased each month from July, 1977 to 21 March, 1978 and then increased in May following spring growth. Belowground biomass increased from July to September but then decreased each month through May. Live and dead culm densities were variable each month with no discernable pattern. Although measurements ceased in May, visual qualitative observations of plants throughout the summer indicated plant growth was normal and similar to marshes in the area.

North Jetty Marsh (site 3)

In the marsh east of the north jetty there was much less oil than that deposited on the fringing marsh on the Houston ship channel. However, on the

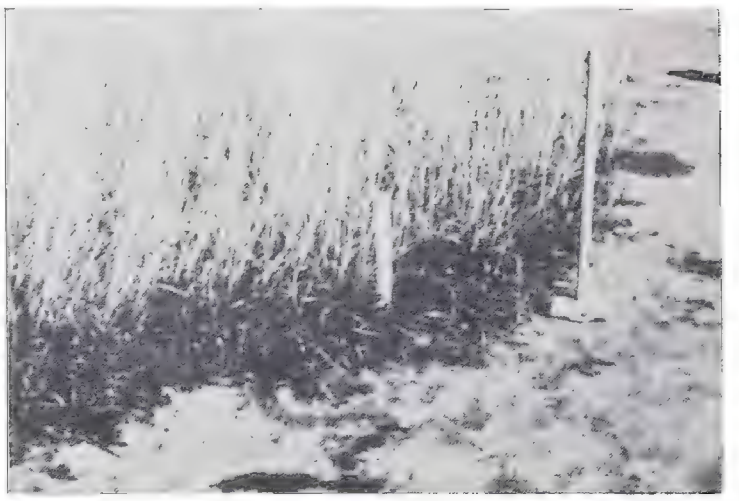

FIG. 2. Oil on smooth cordgrass plants in the site 3 marsh several days after the oil spill October 31, 1977.

water surface there was a continuous layer of oil which spread throughout much of the *Spartina alterniflora* marsh. Plants were colored black from the highest tide marks downward (Fig. 2). The oil settled onto the substrate at low tides and visual observations indicated that the oil actually mixed into the sediment to some extent. However, no gas chromatography or other tests were run to determine amounts. The oil began to disperse into two separate entities within several days leaving a tar-like residue on plants and substrate.

At the time of the oil spill, biomass of plants ranged from 241 to 960 g/m^2 in 4 areas (3 plots in each). By 15 December 1977 some plants that were completely covered by oil had died. The oil which had been present on plants was still evident from the darker color on the lower portion of all stems. However, plants with green stems extending above the oil line were still green except for the seed stalks which normally turn brown in November. Regrowth in all clipped plots was good and was approximately 15 cm high 6 weeks after clipping. Only traces of oil were still evident on the ground. Oil residues disappeared during the spring and early summer leaving no visual evidence of the oil. Growth of plants the following spring and summer showed no visual chronic effects from the oil. During qualitative examinations in May plants were similar in growth to marsh plants of the area, which averaged 441 g/m^2 and 95 cm in height (Tanner 1979). Qualitative estimates of biomass production and height of plants in the fall of 1978 indicated plants were similar in growth and vigor to the preceding year.

DISCUSSION

From observations in both areas, it appeared that if the approximate upper ⅓ of the aerial portions of the plants were free of oil, damage to *Spartina alterniflora* from No. 6 fuel oil was not serious. Total coverage of plants caused death of aboveground parts of plants. Plants were able to regenerate the aboveground biomass if the oil was removed or if the oil covering the soil was light. This agrees with the field studies of DeLaune *et al.* (1979) on the effects of Louisiana crude oil on *Spartina alterniflora.*

Height of tides following similar incidents could be important in determining immediate effects of oil spills. Following extremely high tides most *Spartina alterniflora* plants would probably be covered by oil, thus, causing death of aerial portions of the plants. Of course, subsequent regrowth, may be possible. Baker (1971) reported that *Spartina anglica* survived in good condition 4 successive months of oiling with Kuwait crude oil (experimentally done), but more oilings were detrimental to this species. However, Hampson and Moul (1978) reported the failure of *Spartina alterniflora* to survive a No. 2 fuel oil spill caused by successive applications of the fuel oil on the plants and into the sediments from the flood and ebb of the tide and the natural configuration of the study area which entrapped oil and debris. High No. 2 fuel oil concentrations in the salt-marsh peat were found (Teal *et al.* 1978).

Our results do not indicate the amount of oil a marsh could absorb without damage. Holt, Rabalais, Rabalais, Cornelius, and Holland (1978) reported that recovery and growth of *Spartina alterniflora* was much reduced in heavily oiled areas as compared to lightly affected areas after an oil spill near Port Aransas, Texas.

Since plants were exposed to the oil at the end of the growing season when plants normally begin to senesce, possible toxic effects of oil chemicals may have dispersed prior to regrowth of plants. This seems to agree with findings of Hershner and Moore (1977) who reported the effects of a spill in Chesapeake Bay in February on *Spartina alterniflora.* However, clipped plants did start regrowth immediately without apparent toxicity. Winter growth of *Spartina alterniflora* along with seed germination during the winter occurs frequently in the Galveston area.

Removal of plants did not appear necessary for plants to survive and initiate new growth; also removal of aboveground biomass of the oiled plants did not appear harmful to regrowth. However, most plants were not completely covered by oil. Remobilization of deposited oil from the sediments appeared slight.

CONCLUSIONS

Partial coverage of plants by number 6 fuel oil caused no apparent damage to *Spartina alterniflora* aboveground parts. Complete or near complete coverage of leaves caused death of aboveground parts. However, oiled plants were able to initiate new growth without any apparent ill effects from the oil. Removal of aboveground growth during cleanup operations did not appear to have any adverse effects on plant regrowth the following spring within the cleaned area.

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BLACK MANGROVE, *AVICENNIA GERMINANS*, IN TEXAS: PAST AND PRESENT DISTRIBUTION

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ABSTRACT

Black mangrove, *Avicennia germinans* (L.) L., occurs widely along the Coast of Texas but is concentrated primarily in three central and southern areas. Except for a single record in 1853 from the mouth of the Rio Grande, no other documentation for Texas occurs before the 1930's. Photographic evidence from the early 1900's, however, suggests that mangroves were present along the Texas coast at the turn of the century. A comparison of early and recent aerial photographs indicates that the concentration of black mangroves has increased locally between Matagorda Island and Port O'Connor, Calhoun Co.; in the vicinity of Harbor Island, Nueces Co. and in the Port Isabel-South Bay area, Cameron Co. from the 1930's to the late 1970's. Field reconnaissance in 1979–1980 documented the northernmost distribution at Galveston Island and the southernmost at Brazos Island near the mouth of the Rio Grande.

INTRODUCTION

Questions have arisen concerning the present distribution and historical presence of black mangrove, *Avicennia germinans* (L.) L., on the Texas coast. Despite a single herbarium record in 1853, there has been little documentation of its continuous presence from that time to the 1930's. The evidence since the early 1930's suggests that mangroves have been in Texas continuously during the past 50 years but the records are incomplete concerning its overall distribution and abundance.

Four mangrove species occur in the northern Gulf region but only the black mangrove extends into Texas, Louisiana and Mississippi. Seedlings of the red mangrove, *Rhizophora mangle* L., are washed ashore in a viable condition on Texas beaches (McMillan 1971, Gunn and Dennis 1973), but no naturally established plants have been observed. The white mangrove, *Laguncularia racemosa* (L.) Gaertn., and the button mangrove, *Conocarpus erectus* L., occur with both the black and red mangrove approximately 300 km south of the Texas border in northeastern Mexico at LaPesca, Tamaulipas (Lot-Helgueras *et al.*, 1975) and also on the southern Florida Gulf Coast (Davis 1940).

For an evaluation of the present and past distribution of black mangrove in Texas, diverse types of information were examined. Herbarium records at the

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University of Texas at Austin were checked to determine the dates and localities of this form of plant documentation. A field reconnaissance was conducted in 1979–80 along the northern coast from Sabine Pass at the Louisiana border to Matagorda Island, along the central coast in the vicinity of Port Aransas and along the southern coast from Port Isabel to Brazos Island, immediately north of the Rio Grande. Aerial photographs that were recorded along the Texas coast in 1930–40's and the 1970's were compared for an estimation of the changes in mangrove distribution in the three areas of its present major concentration in Texas.

PRESENT DISTRIBUTION AND RELATIVE ABUNDANCE ALONG THE GULF COAST OF TEXAS

Northern Coast: Sabine Pass to Matagorda Bay

Avicennia is sparse along the northern coast and no plants are presently recorded between Galveston Island and the Louisiana border (Fig. 1). Although mangroves were collected at Sabine Pass in 1939, 1948 and 1954 (Table 1), none was observed in 1979. Observations by other workers in the vicinity of the Louisiana border during the past ten years (Texas Parks and Wildlife Department, U.S. Fish and Wildlife Service and Texas A&M University Remote Sensing Center, personal communications, 1979–1980) did not indicate the recent presence of mangroves at Sabine Pass.

The most northerly occurrence of black mangrove at present is on Galveston Island. On the northeast end of the island, they are scattered within a narrow band of *Spartina* salt marsh between the Coast Guard Station and the outer beaches (Fig. 2). Numerous dead plants within this population suggested that recent over-winter low temperatures may limit the extent of mangroves along the northern coast. One of the largest living plants was examined for growth ring data and proved to be less than seven years old.

Scattered mangroves are reported near the west end of Galveston Island. These plants were observed by the Texas A&M University Remote Sensing Center (Wally Snell, personal communication, 1980) on low islands immediately west of San Luis Pass. The remainder of the coast between Galveston Island and Matagorda Bay is primarily composed of sandy beaches which do not provide suitable habitats for mangrove establishment.

Central Coast: Matagorda Bay to Corpus Christi Bay

The northernmost dense concentration of *Avicennia* in Texas occurs near Port O'Connor in Calhoun Co. The plants occur on the numerous low islands between the northeast end of Matagorda Island and Port O'Connor, immediately west of Cavallo Pass (Fig. 3). The mangroves are estimated to occupy 1500 hectares (Benton *et al.*, 1977) but the field reconnaissance indicated that the relative abundance varies widely throughout the area. The mangroves are usually mixed with *Spartina*, *Batis* and *Salicornia* on the outer fringes of the

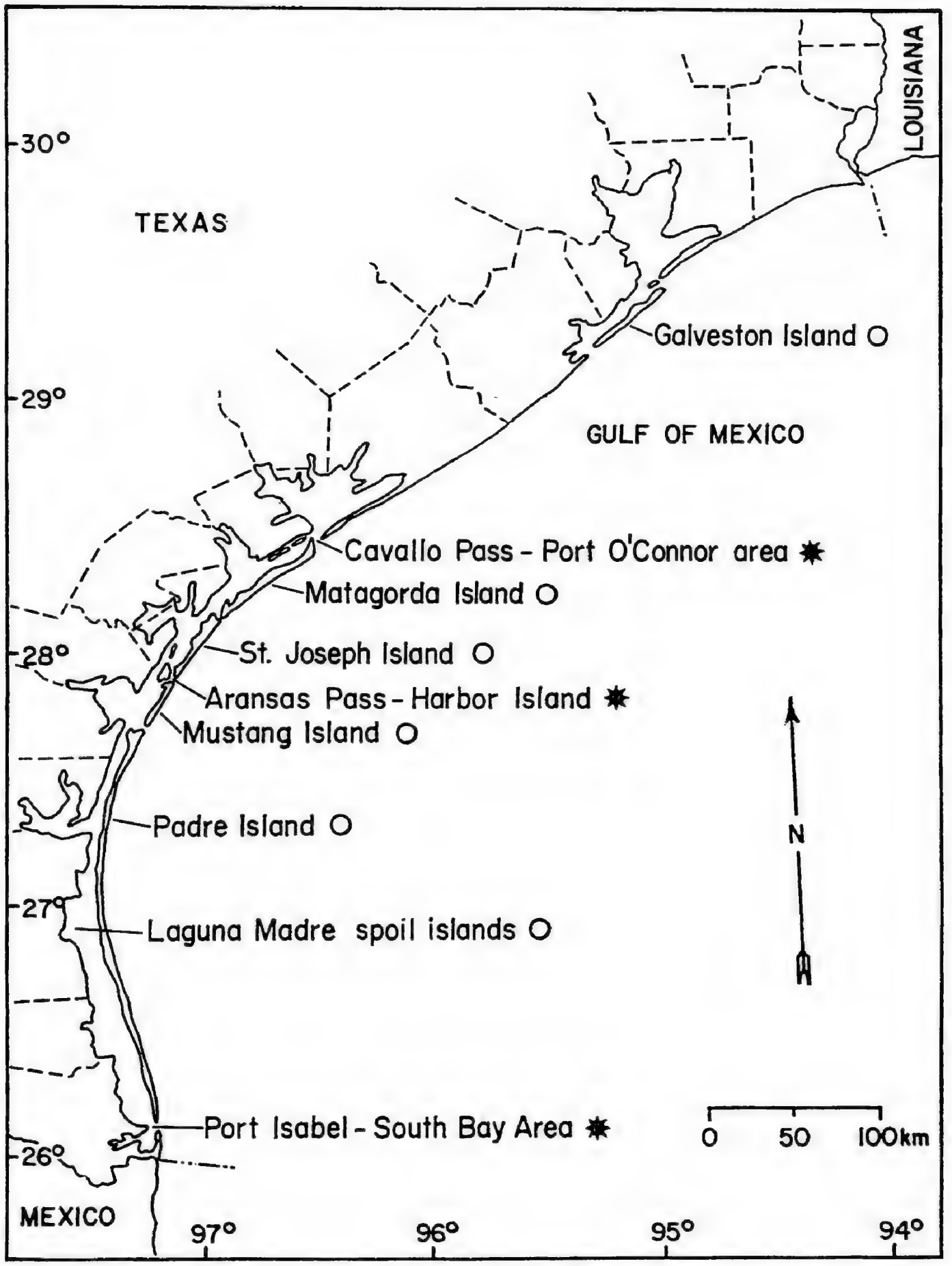

FIG. 1. Map of the Gulf Coast of Texas showing the present abundance of black mangrove, *Avicennia germinans*: o, scattered; *, abundant.

TABLE 1

Chronological listing of black mangrove, *Avicennia germinans*, collections on the Texas coast.[1]

Date	County	Place[2]	Collector
1853	Cameron	mouth of Rio Grande	A.C.V.Schott (Torrey 1859)
1931	Cameron	sandy flats near waterline on bay	R. Runyon 1420
1933	Cameron	Clark Island,Boca Chica	E. Clover 715
	Nueces	Harbor Island	E. Whitehouse
1937	Cameron	near Boca Chica	R. Runyon 2173
1939	Nueces	Port Aransas	B.C. Tharp
	Jefferson	Sabine Pass	B.C. Tharp
1940	Cameron	Del Mar Beach	H.B. Parks 1724
	Cameron	Clark Island	C.L. and A.A. Lundell 8760
1941	Cameron	Brazos Santiago Is.	R. Runyon 2812
1945	Cameron	Point Isabel	R. Runyon 4031
1948	Jefferson	-	Mrs. B. Reed
1950	Cameron	Boca Chica	G.L. Webster & R.L. Wilbur 3035
1952	Cameron	Port Isabel	Tharp,Gimbrede & Johnston 52525
1954	Nueces	Lighthouse (Harbor) Island	H.H. Hildebrand & M.C. Johnston 541270
	Jefferson	7 miles west of Sabine Jetty	H.H. Hildebrand 3
1960	Cameron	½ mi. west of Boca Chica Beach	A. Traverse 1812
1962	Cameron	Padre Island, east of Port Isabel	Correll, Lundell & Johnston 25539
1965	Cameron	Point Isabel	R. Runyon 5897
1966	Cameron	Port Isabel	D.S. Correll 32372
1967	Cameron	bay inlet crossed by F.M. 1792	J.R. Crutchfield 2895
1980	Galveston	northeast end of Galveston Island	C.L. Sherrod 2
1980	Calhoun	Saluria Island	C.L. Sherrod 4
1980	Cameron	Brazos Island, near Boca Chica	C. McMillan 8001

[1] All collections except that of Schott are in the University of Texas at Austin Herbarium (TEX).

[2] Various collections in Cameron County that are listed as Santiago Brazos Island, Brazos Island, Clark Island and Boca Chica may refer to the same general area that is accessible by highway at the south end of Brazos Island, a peninsula in 1980 that is intermittently separated from the mainland by the opening of a small pass, Boca Chica, from South Bay to the Gulf.

islands and do not form extensive dense stands (Fig. 4). Field observations indicated that numerous seedlings occurred throughout the area and that mangroves were colonizing new shorelines in Espiritu Santo Bay.

Avicennia plants are scattered along Espiritu Santo Bay on the margins of Matagorda Island and St. Joseph Island to the south. A few areas of less than one hectare of heavy concentration were noted on color infrared aerial photo-

FIG. 2. Scattered mangroves in the *Spartina* marsh on the northeast end of Galveston Island. Mangroves are under 1 m in height in this 1980 photograph.

graphs (1979), notably on Vandeveer Island, just west of the old Matagorda Island Air Force Base, and within various washover fans on the more southern parts of the islands.

A major concentration of mangroves occurs near the southern end of St. Joseph Island on a tidal delta, Harbor Island (Fig. 5). In this area near Port Aransas, Nueces Co., the plants were conspicuous on approximately 600 hectares (Benton *et al.*, 1977).

Although the densest mangrove concentration is on the northeast part of Harbor Island (Fig. 6), plants are scattered on the numerous islands that lie near it in Aransas and Redfish Bays. The plants are not confined to the islands but occur on the mainland bay margins 10 km west of Harbor Island near the city of Aransas Pass. Scattered plants can also be found along the bay margins of Mustang Island and Padre Island, barrier islands south of St. Joseph Island.

Southern Coast: Laguna Madre to the Rio Grande

The mangrove populations of the southern coast occur primarily as scattered heavy concentrations in the Port Isabel-South Bay area of Cameron Co. The largest single expanse is on the south shore of San Martin Lake, about 16 km west of Port Isabel along the Brownsville Ship Channel (Fig. 7, 8). Plants are also widely scattered on the bay margins of Padre Island and the numerous spoil islands bordering the Gulf Intracoastal Waterway in the Laguna Madre from Corpus Christi Bay to Port Isabel. The southernmost mangroves recorded in 1980 (Table 1) were scattered along the bay margins of South Bay and at Boca Chica on Brazos Island, several km north of the mouth of the Rio Grande.

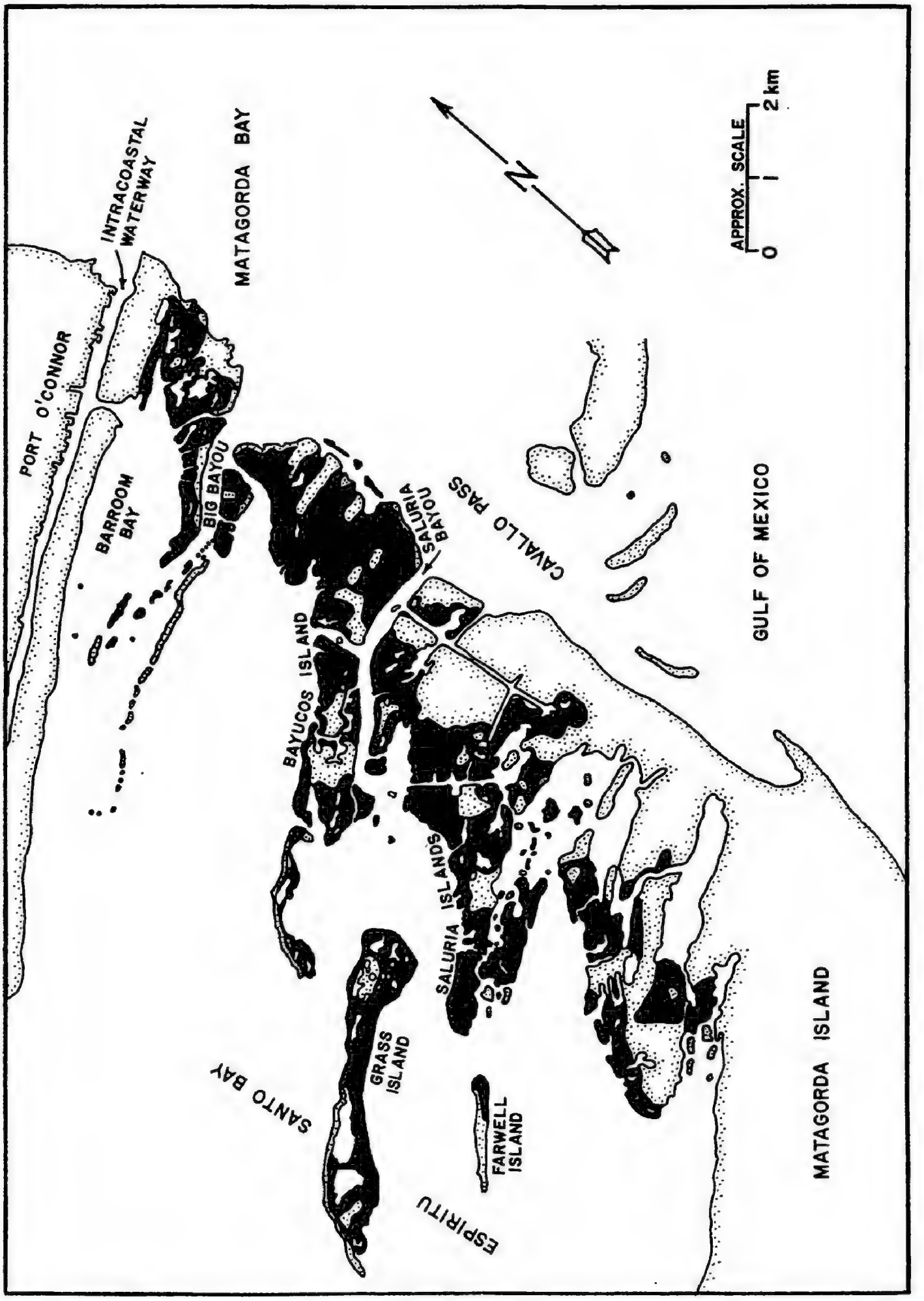

FIG. 3. Occurrence of dense mangrove stands (blackened areas) in the Cavallo Pass-Port O'Connor areas as indicated by 1979 infrared aerial photographs. Scattered individuals and small stands that were not detectable on the aerial photographs are not indicated.

FIG. 4. Mangroves near Big Bayou in the Cavallo Pass-Port O'Connor area. Plants are under 1 m in height in this 1980 photograph.

The total area covered by mangroves in the Port Isabel-South Bay area was estimated as 500 hectares (Fig. 7) but of this total, ca. 300 hectares occur in the San Martin Lake region. Numerous seedlings occur in the vicinity of San Martin Lake and have colonized roadside ditches and other moist areas not influenced by tidal action.

PAST DISTRIBUTION IN TEXAS

Although *Avicennia* was collected in Texas in 1853 (Table 1), it was apparently not collected again or mentioned in the written record from 1859 (Torrey) until 1931. The 1853 collection by A. C. V. Schott at the mouth of the Rio Grande was recorded by Torrey, but the earliest collection at the University of Texas at Austin is from Cameron Co. in 1931 (Table 1).

Photographic evidence indicates the presence of black mangroves in Texas at the turn of the century. Photographs in the vicinity of Harbor Island recorded in the early 1900's indicate isolated plants. Aerial photographs taken in the 1930–40's show well developed stands of mangroves in Calhoun, Nueces and Cameron Counties (Figs. 9, 10, 11) and suggest that they were present long before the earliest collection of 1931.

Distributional data are fairly continuous after 1931 (Table 1). Although most records are from Nueces Co. (Harbor Island) and Cameron Co., mangroves were collected at Sabine Pass, as indicated above, from 1939 to 1954. Vines (1960) reported *Avicennia* from the east end of Galveston Island near the stone breakwater where they were recorded in 1980.

Apparently the first report of mangroves in Calhoun Co. was that of Hartman and Smith (1973). Their survey was primarily of Matagorda Island, but

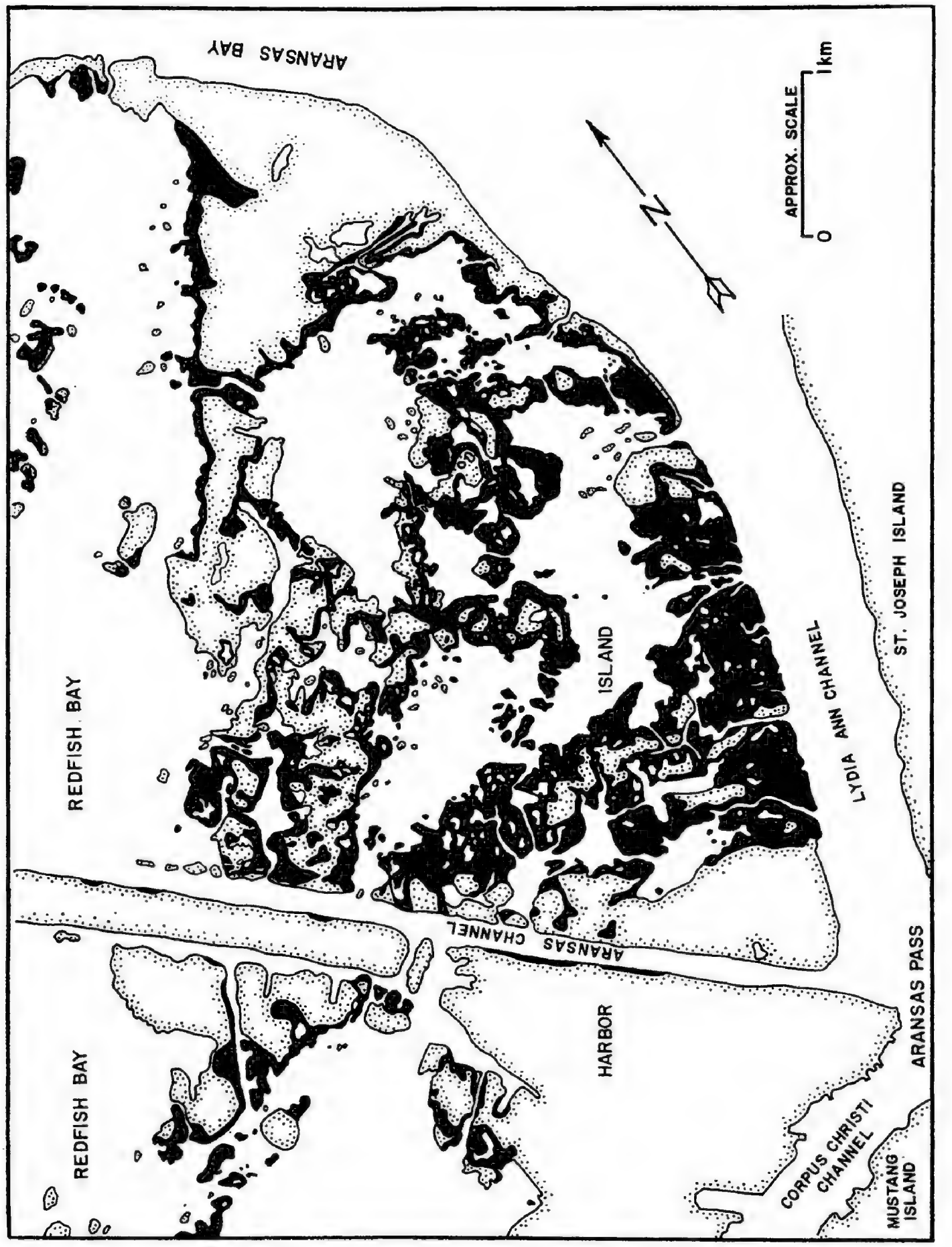

FIG. 5. Occurrence of dense mangrove stands (blackened areas) on Harbor Island, Nueces Co., as indicated by 1979 infrared aerial photographs. Scattered individuals and small stands that were not detectable on the aerial photographs are not indicated.

FIG. 6. Mangroves on Harbor Island in 1969. The mangroves are mostly between 1 and 2 m in height. Pneumatophores are conspicuous along the margin of this tidal creek north of the lighthouse.

they mentioned reports by local residents of extensive mangrove swamps on Saluria and Bayucos Islands where mangroves are currently abundant. These mangrove stands were indicated in the aerial photographs of the 1930's (Fig. 9).

Mangrove distribution in the Harbor Island area of Nueces Co. has been well documented since the 1930's. The causeway from the city of Aransas Pass on the mainland to Port Aransas on Mustang Island crosses Harbor Island and has made this mangrove area accessible to many collectors (Table 1, Fig. 10). Although the section visited by the causeway is separated from the major portion of Harbor Island by a dredged waterway, the Aransas Channel, the main concentration of mangroves is readily accessible by boat from either the Aransas Channel or the Lydia Ann Channel which separates Harbor Island from St. Joseph Island. The lighthouse on Harbor Island has made this tidal delta a focal point for visitors since its construction in the mid-1880's. R. A. Hoover (unpublished data, 1966) conducted a vegetational study of Harbor Island and his photographs record the common occurrence of mangroves at that time. McMillan (1971; unpublished data, 1968–1980) studied the environmental tolerances of the black mangrove from Harbor Island and observed the distribution of mangroves in 1968 as being restricted mainly to Harbor Island. Only a few plants were observed in Port Aransas on Mustang Island in 1968, but during the 1970's mangroves had become widely distributed on other islands as well as along the mainland bay margins. Jones (1975) noted their presence along Packery Channel that divides Mustang and Padre Islands near Corpus Christi. In addition, Jones stated that *Avicennia* had been reported from the mouth of the Aransas River along the bay margin of Copano Bay of Refugio and Aransas

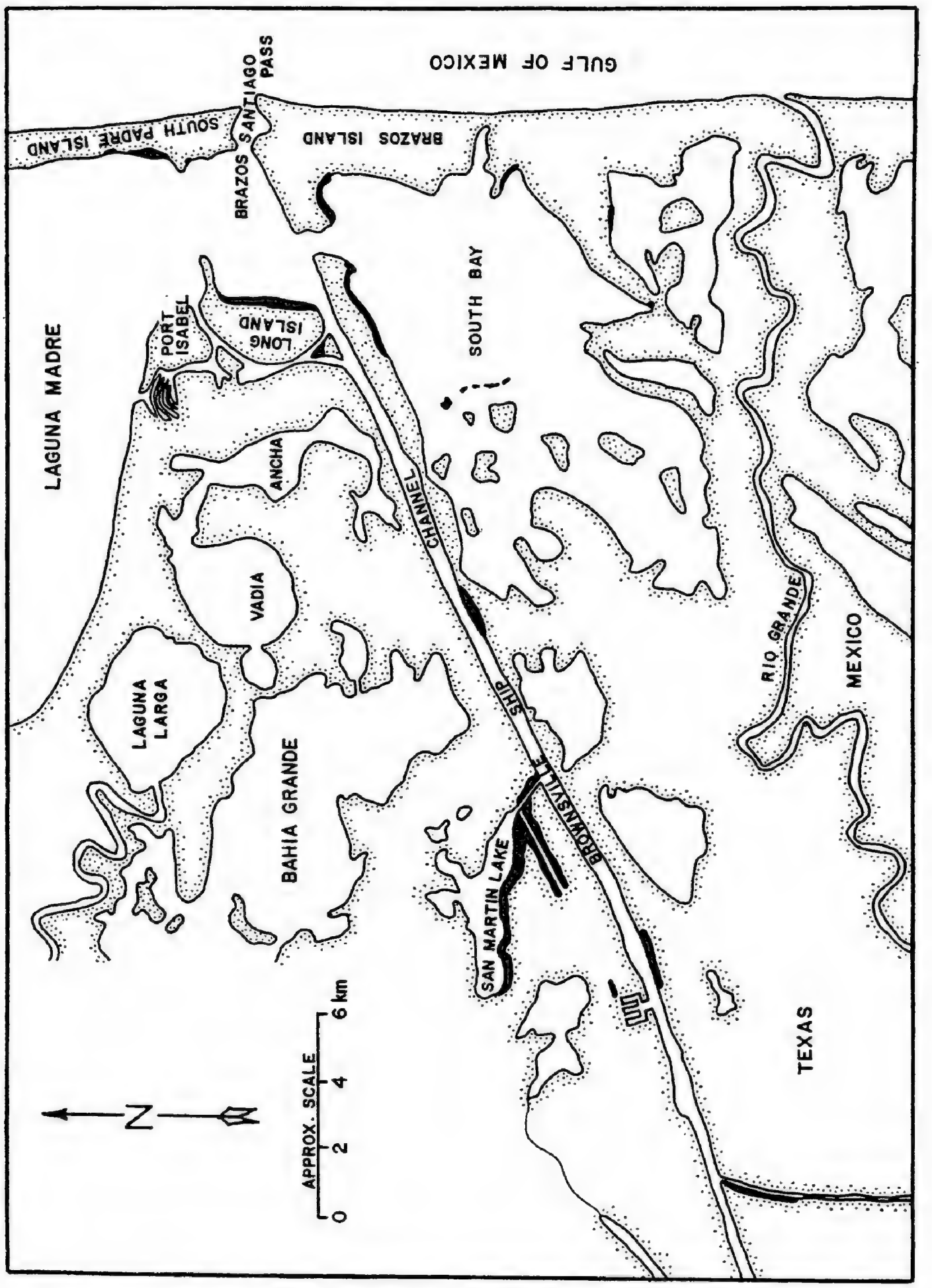

FIG. 7. Occurrence of dense mangrove stands (blackened areas) in the Port Isabel-South Bay area, Cameron Co., as indicated by 1979 infrared aerial photographs. Scattered individuals and small stands that were not detectable on the aerial photographs are not indicated.

FIG. 8. Mangroves along the south shore of San Martin Lake adjacent to the Brownsville Ship Channel. Mangroves in the foreground are scattered along a roadside ditch and range between 1 and 2 m in height in this 1979 photograph.

Counties, but that report has not been verified. The dense concentration of mangroves on Harbor Island has probably remained a persistent stand throughout this century and has produced the seed that has led to the wide colonization of adjacent islands during the 1970's.

The Port Isabel-South Bay area has been visited by numerous collectors (Table 1). Although, as indicated above, the first report in the literature was from the mouth of the Rio Grande (Torrey 1859), Clover (1937) described mangroves on Clark and Brazos Islands. Johnston (1952, 1955) reported *Avicennia* from the margins of the Brownsville Ship Channel, the northern end of Horse Island, an area south of Loma del Ballo and in the vicinity of Port Isabel. McMillan (unpublished data) noted the presence of mangroves in 1969 on Long Island, west of Port Isabel, and that stand has been continuously present to 1980. Long Island has recently been put into tourist use and the structure of the island has been altered slightly. The continued presence of mangroves at this site may be jeopardized by this altered use of the island. McMillan also noted extensive stands of mangroves along the Brownsville Ship Channel and noted from 1969 to 1980 that there has been some expansion of mangrove distribution in the vicinity of San Martin Lake.

DISCUSSION

Despite claims that the black mangrove is a relatively recent introduction to Texas, the historical record suggests that it may have been continuously present along the Gulf Coast but that its overall distribution has expanded and contracted in response to variations in environmental conditions. The three major

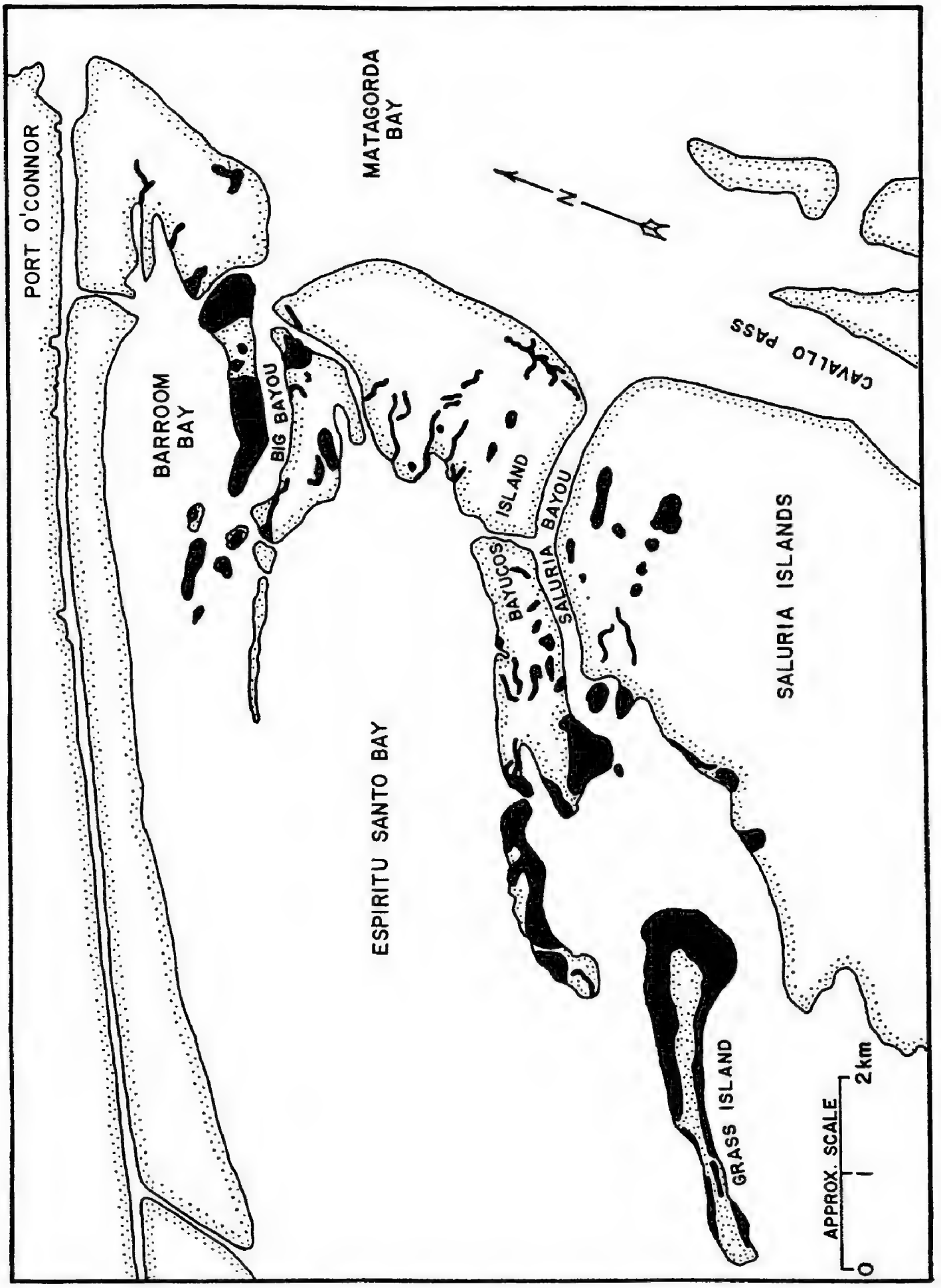

FIG. 9. Distribution of black mangrove (blackened areas) in the Cavallo Pass-Port O'Connor areas as indicated on black and white aerial photographs taken in the 1930's.

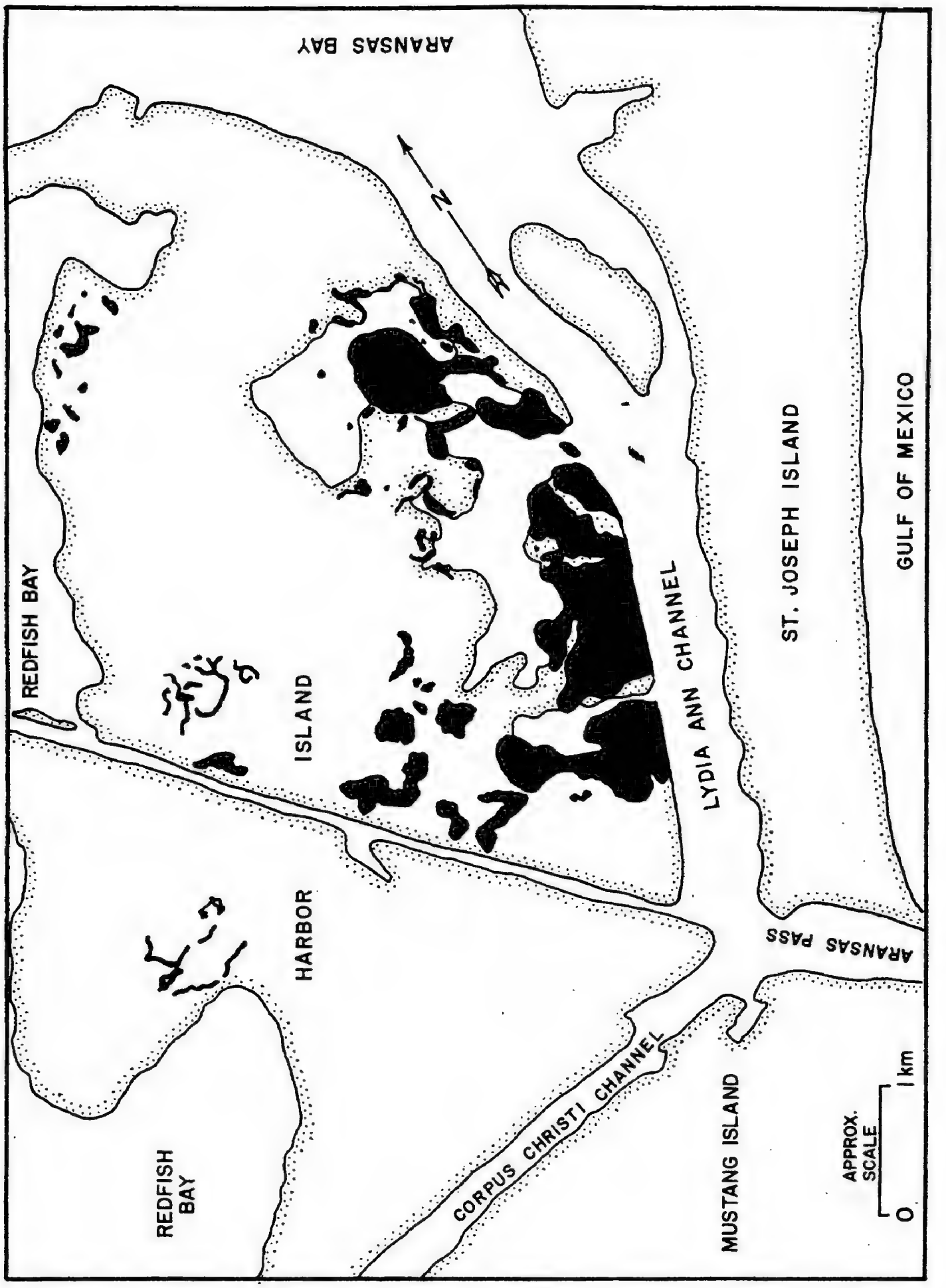

FIG. 10. Distribution of black mangrove (blackened areas) on Harbor Island as indicated on black and white aerial photographs taken in the 1930's.

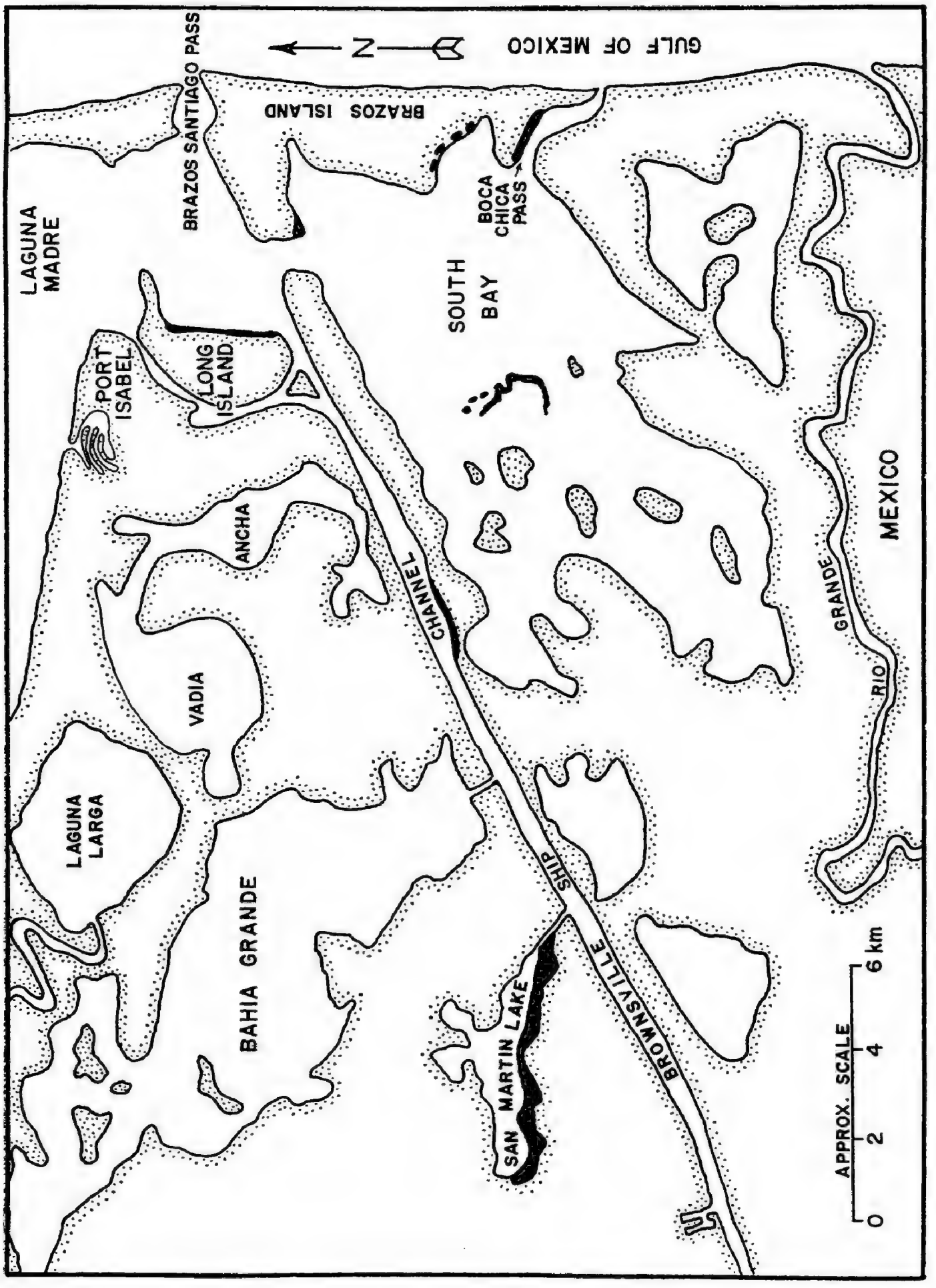

FIG. 11. Distribution of black mangroves (blackened areas) in the Port Isabel-South Bay area as indicated on black and white aerial photographs taken in the 1940's.

concentrations in 1980 at Cavallo Pass in Calhoun Co., at Harbor Island in Nueces Co. and in the Port Isabel-South Bay area of Cameron Co. may represent the points of continuous mangrove occurrence. During periods of drought and general hypersaline conditions in surrounding areas, the mangroves may have been locally confined (McMillan 1975a) but during periods of higher rainfall, the mangroves may have been actively colonizing surrounding areas as exemplified by the 1970's. The comparison of aerial photographs of the 1930–40's and the late 1970's indicates major concentrations of mangroves in the three central and southern areas of the Texas coast throughout this century.

The three areas of major mangrove concentration have similar characteristics. Each locality is composed of low relief islands or shorelines just inside major passes through the sandy barrier islands. The mangroves in the Cavallo Pass area are largely confined to the low islands to the northwest of the pass and immediately behind Matagorda Island. Harbor Island lies directly west of the barrier island, St. Joseph, and represents a tidal delta which formed in relation to Aransas Pass. The pass migrated through time but was stabilized with jetties at its present location leaving Harbor Island slightly offset to the north. Harbor Island was bisected by the Aransas Channel that was dredged to the city of Aransas Pass with the major part of the mangroves on the northern part of the island. The southern mangrove concentration in Texas may have focused on Port Isabel, directly opposite Brazos Santiago Pass which separates the barrier islands of Padre on the north and Brazos on the south. With the dredging of the Brownsville Ship Channel, the mangrove distribution was extended beyond Port Isabel and South Bay. At present the major concentration of mangroves is west of Port Isabel at San Martin Lake but the population on Long Island at Port Isabel may represent the original stand. The positions behind barrier islands are the most favorable for mangroves on the Texas coast because they provide a combination of shallow or tidal, low-energy habitat that is protected from hypersaline conditions by regular inflows of stable oceanic water. In addition, these areas provide a slight thermal barrier to low winter temperatures by being protected on the north side by large bodies of water, Matagorda Bay (Cavallo Pass area), Aransas Bay (Harbor Island) and Laguna Madre (Port Isabel).

The mangroves of Texas represent populations that have been genetically selected for survival under winter temperatures that are colder than those experienced by more tropical populations of the same species. The studies of McMillan (1975b) and Markley and McMillan (unpublished data) show that mangroves from either Harbor Island or the Port Isabel-South Bay area (plants from Cavallo Pass were not included in the studies) can withstand exposures to low chilling temperatures (2–4° C) that produce considerable plant damage to the black mangrove of more tropical origin in the southern Gulf of Mexico and the Caribbean. Populations of *A. germinans* from the diverse latitudes along the Gulf of Mexico showed an adaptive gradient to uniform chilling conditions with Texas plants being the most chill tolerant. The photoperiod and temperature of the growing conditions that preceded the chilling tests did not alter the

tolerance of the experimental plants, which suggested that differentiation to chilling in mangroves is based on inherited properties. Through natural selection, the mangroves of Texas and the northern Gulf Coast have adaptive advantages for survival in habitats that are periodically exposed to chilling conditions.

The adaptive selection of mangroves in northern Gulf Coast habitats suggests that they have not been recently introduced to Texas from a more tropical site. Although only one collection was recorded in Texas in the 1800's, as indicated above, there are collections throughout the 1800's in coastal areas of Louisiana, Mississippi, Florida and Mexico (Moldenke 1960). Plants that have the adaptive properties for survival at Grande Isle, Louisiana or in Mississippi should be able to survive in Texas. The nearly continuous geologic evidence of mangroves in Florida since the last oceanic stillstand, 3000–4000 years ago (Scholl 1964), indicates that *Avicennia* has probably had a continuous presence in the northern Gulf region throughout that time.

Geologic evidence during the Pleistocene indicates that mangroves were more equatorially restricted than they are today (Bartlett and Barghoorn 1973, Berry 1925). Preceding the Pleistocene, mangal vegetation was probably continuously present for millions of years throughout the northern Gulf region. Although it is not definitely known when present day forms developed, fossil mangroves from the Eocene show very close similarities to modern plants (Berry 1916, 1924). The fluctuating climate of the Pleistocene may have led to the natural selection of an adaptive gradient in mangroves for the diverse habitats along the Gulf of Mexico.

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